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RATE OF ABSORPTION OF SOIL CONSTITUENTS AT SUCCESSIVE STAGES OF PLANT GROWTH

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Data derived from the periodic cuttings of a crop of barley in 1916 were used in a previous paper (*1*)[2] to develop certain general relations between the amounts of soil constituents acquired by the plant at various stages of growth and those present in the water extracts of soils. It is evident that the value of conclusions drawn from such data is somewhat limited if based upon results obtained from a single soil. On the other hand, the detailed and laborious studies necessary in such inquiries may not be indefinitely repeated; and further work of this kind was not originally contemplated. In the course of the work referred to, however, certain aberrations in the data appeared to indicate errors or to lead to conclusions of such an extraordinary character as to demand additional experimental verification, so a further study was carried out the following season, 1917. The principal object of this paper is to present the result then obtained. Since, however, these justify the data from the earlier work and corroborate certain important conclusions logically deducible therefrom, but not hitherto published, the complete results of the periodic harvests from both studies will be considered.

CONDITIONS OF THE EXPERIMENTS

The details of the experiments were formulated primarily to insure:

That the individual plants in each experiment should have access to an equal volume of soil.

That there should be no opportunity for loss of soil constituents by drainage or leaching, or gain from the constituents of rain or irrigation water.

That there should be no opportunity for removal of plant constituents by the washing off of effloresced or soluble constituents by rain.

[1] Thanks are extended to Messrs. A. W. Christie and J. C. Martin for performing the analyses reported herein and for assistance in the computations, etc., and to Prof. G. R. Stewart for supervision of the cultural arrangements and harvesting of the plants.

[2] Reference is made by number (italic) to "Literature cited," p. 72.

The crop was the selected strain of Beldi barley used in much of the previous work of this laboratory. The plants were grown on a silty clay loam soil (*1c*) in 1916 and on a fine sandy loam soil (*15*) in 1917.

In the 1917 experiment the soil, made as homogeneous as possible by sifting and mixing, was installed in 8 tight galvanized iron boxes or containers with a surface area of 30 by 60 inches each and a depth of 18 inches. Two of the containers were equally divided by a lateral partition, giving a total of 10 independent compartments. The soil in one of the large containers was used as a control plot, and the other plots were used for growing the crop. The plants were placed 6 inches apart in the row with 6 inches between rows. Thus there were 50 plants to each of the large containers and 25 plants to each of the small containers, with equal volumes, weights, and superficial areas of soil per plant. The plants were cut at intervals of two weeks throughout the season, beginning with the third week from planting. At the same time samples were drawn and water extractions made from soil in the control plot container and from the containers being cropped. No further soil samples were taken from any container after the plants were removed therefrom. The containers were compactly arranged, insulated from heat fluctuations except at the surface, and protected from birds and rodents. All plots were watered with distilled water only and protected during the infrequent rains by rubber covers placed on wire frames. The mechanical arrangement and methods of sampling soils were in all respects the same as those described in greater detail in connection with other experiments from this laboratory (*8*). In order to obtain sufficient material for the chemical studies, we used the contents of two of the large containers for the first cutting, one large container for each of the three succeeding cuttings, and one small container each for the last four cuttings. The minimum number of plants embraced by any cutting was 23 at the fifteenth week from planting, in which instance 2 plants failed to develop after thinning.

The procedure in the 1916 experiment was similar to that of 1917. A minor difference which should be noted was that the containers for the cropped soil in 1916 were of wood and varied several inches in each dimension from the iron containers used in the work of the following year. A more important difference lies in the fact that in attempting to economize equipment and soil, which was brought from a distance at considerable expense, we used two containers of soil, one cropped and one uncropped, which had been in place and were grown to a crop of barley in the year 1915. One of these was used as a control plot and one for the determination of total yield at the end of the season. Subsequent determinations of the water-extractable matters from these soils showed somewhat higher concentrations than those from the soils in the newer containers from which the successive cuttings were made. This could have had no effect on the data obtained for the plant, inasmuch as the periodic cuttings were all made on soil assembled, mixed, and installed

at one time, but may be regarded as vitiating the data obtained from the soils for certain other purposes. To obviate criticism on this point we shall in the present paper confine our conclusions as to the soil to those obtained from the data of the 1917 experiment, although these are in all general relations confirmed by the work of the preceding year.

CHEMICAL TECHNIC IN THE EXPERIMENTAL WORK

The water extractions of the soils and the analyses of the extracts were made by the methods described by Stewart (*8*); the analyses of the plants were made by the usual methods of treatment for nitrogen and plant ashes, with proper precautions to prevent the loss of partially volatile constituents.

MECHANICAL DIVISION OF PLANTS

Since the object of the investigation was to bring out certain general relations between the type crop and the soil, it was not deemed desirable or profitable to make a complete separation of the plants based on their more minute anatomical structure. The well-known and substantial differences in composition between the heads of grain crops and the vegetative tissues seemed, however, to require the separation of the plant into at least these two parts; furthermore the roots obviously deserve separate consideration. The procedure actually followed was to remove the entire plant with as much of the roots as possible. In all cuttings after the heads had formed these were separated from the vegetative portion, designated stems and leaves. The roots of all plants were severed by a lateral cut through the base of the crown. As separated, this portion of the plants therefore included a small portion of the lower part of the crown. The roots so recovered included only a small proportion of the finer rootlets. Most of these had broken loose from the plants and were to be found throughout the soil in very fine and fragile strands which it is hopeless to expect to remove in their entirety.

The results reported hereafter on the upper part of the plant make it appear probable that a study of root composition would give important data on the mechanism of plant absorption, but that such a study should be based on very exact measurements of the quantities and composition of the roots. For this purpose natural soils, even when the roots are washed free, do not appear to offer the best medium for growing the plants, inasmuch as the data would always be subject to the criticism that the recovery was incomplete, or that the roots had sustained losses of solutes from the washing or gains from adhering soil particles. On this account we abandoned the idea of making a chemical study of the roots collected in the plot experiments, but will present evidence from other sources as to the effect of root composition on our conclusions.

PRESENTATION OF DATA

As a matter of record the original data are given in terms of yields and of the composition of the moisture-free material. (See Tables I and II.)

All figures are, however, recomputed in terms of the absolute amounts of the constituents reported. These are expressed both as grams per plant and as parts per million of soil. (See Tables III and IV.)

Inasmuch as the succeeding discussion centers about the graphs, presented in some detail, a word concerning these is perhaps necessary. The 2-week interval between cuttings, used for the most part, appears to have been sufficiently short to bring out the more important characteristics of growth and absorption. It will be noted, however, that in the 1916 experiment the first cutting did not take place until six weeks after planting. The fact that the plants did not appear above ground for several weeks and the further fact that the earlier harvests of the 1917 experiment showed very characteristic changes, indicate that the use of a straight line to cover this period in the 1916 graphs is highly artificial. However, the method is consistent in that we have connected only known points; and the facts as to absorption and growth at this stage are sufficiently clarified by the 1917 experiment.

Since our data are derived from two relatively independent studies of the growth of barley on two very different soils in two different calendar years, it is obvious that differences may be expected to appear which are equally assignable to one or another of the conditions of growth such as soil, season, etc. Our present purpose is not to account for such differences, but to call attention to certain similarities which are rendered all the more striking in view of the great differences in the yields actually obtained.

Table I.—*Barley at successive stages of growth*

GROWN ON SILTY CLAY LOAM SOIL (1C) IN SEASON OF 1916

Date.		Age from planting (in weeks).	Number of plants.	Description.	Average weight per plant (in grams). Total.	Moisture.	Dry matter.	Percentage of moisture.	Percentage of dry matter.	Analyses of moisture-free material. Percentage of nitrogen.	Percentage of phosphorus.	Percentage of potassium.	Percentage of calcium.	Percentage of magnesium.
June	12	6	69	Entire, except roots [a]	23.84	21.62	2.22	90.70	9.30	3.71	0.50	5.40	0.47	0.54
	26	8	49	do	47.96	39.82	8.14	83.02	16.98	1.66	.41	3.70	.37	.34
July	10	10	42	do	48.83	36.73	12.10	75.23	24.77	.91	.29	1.87	.25	.27
	24	12	29	do	48.66	32.80	15.86	67.40	32.60	.77	.25	1.23	.23	.25
Aug.	7	14	28	do	47.43	30.21	17.22	63.70	36.30	.76	.26	1.17	.19	.22
	21	16	38	do	29.45	9.53	19.92	32.35	67.65	.71	.28	1.24	.22	.22
	28	17	87	do	23.15	3.00	20.15	16.96	87.04	.71	.28	1.19	.18	.22
July	10	10	42	Stems and leaves	42.12	32.08	10.04	76.14	23.86	.80	.29	2.09	.28	.29
	24	12	29	do	32.55	23.38	9.17	71.82	28.18	.45	.16	1.71	.34	.31
Aug.	7	14	28	do	30.04	21.79	8.25	72.53	27.47	.27	.10	1.89	.33	.28
	21	16	38	do. [b]	15.58	3.84	11.74	24.66	75.34	.27	.15	1.77	.33	.27
	28	17	87	do. [b]	13.04	1.42	11.62	10.84	89.16	.24	.13	1.74	.28	.24
July	10	10	42	Heads	6.72	4.67	2.05	69.50	30.50	1.30	.32	.81	.12	.15
	24	12	29	do	16.10	9.41	6.69	58.46	41.54	1.22	.37	.57	.07	.18
Aug.	7	14	28	do	17.40	8.43	8.97	48.46	51.54	1.22	.40	.51	.06	.17
	21	16	38	Grain	13.87	5.68	8.19	41.00	59.00	1.34	.47	.49	.05	.15
	28	17	87	do	10.12	1.59	8.53	15.88	84.12	1.36	.49	.44	.05	.18

[a] See subsequent data and discussion concerning effect of omitting roots.

[b] Stems and leaves include chaff from grain on this date.

TABLE II.—*Barley at successive stages of growth*

GROWN ON SANDY LOAM SOIL (15) IN SEASON OF 1917

Date.	Age from planting (in weeks).	Number of plants.	Description.	Average weight per plant (in grams). Total.	Moisture.	Dry matter.	Percentage of moisture.	Percentage of dry matter.	Analyses of moisture-free material. Percentage of nitrogen.	Percentage of phosphorus.	Percentage of potassium.	Percentage of calcium.	Percentage of magnesium.
May 21	3	97	Entire, except roots[a]	0.7630	0.6867	0.0763	90.00	10.00	6.16	0.79	6.16	0.92	0.92
June 4	5	49	....do	6.652	5.879	.773	88.40	11.60	5.51	.60	5.96	.78	.47
18	7	50	....do	33.140	29.042	4.098	87.59	12.41	3.27	.55	4.87	.59	.41
July 2	9	49	....do	81.80	70.01	11.79	85.59	14.41	2.58	.35	3.51	.52	.31
16	11	25	....do	76.80	58.56	18.24	76.09	23.91	1.04	.27	1.50	.29	.17
30	13	25	....do	85.88	58.09	27.79	67.64	32.36	.87	.25	1.15	.28	.14
Aug. 13	15	23	....do	107.90	71.17	36.73	65.95	34.05	.97	.24	1.21	.29	.18
Sept. 6	18+	25	....do	57.60	28.17	29.43	48.91	51.09	1.22	.31	1.22	.31	.18
July 2	9	49	Stems and leaves	78.85	67.755	11.095	85.93	14.07	2.62	.35	3.63	.55	.32
16	11	25	....do	66.72	51.63	15.09	77.38	22.62	.93	.26	1.61	.32	.18
30	13	25	....do	63.36	44.34	19.02	69.98	30.02	.61	.20	1.36	.36	.14
Aug. 13	15	23	....do	70.78	49.16	21.62	69.46	30.54	.47	.12	1.70	.43	.18
Sept. 6	18+	25	....do.[b]	38.84	23.18	15.66	59.68	40.32	.50	.12	1.94	.57	.23
July 2	9	49	Heads	2.939	2.247	.692	76.46	23.54	1.98	.38	1.52	.12	.15
16	11	25	....do	10.08	6.938	3.142	68.84	31.16	1.58	.31	1.00	.15	.13
30	13	25	....do	22.52	13.752	8.768	61.07	38.93	1.44	.36	.70	.11	.13
Aug. 13	15	23	....do	32.74	17.63	15.11	53.85	46.15	1.69	.42	.50	.09	.17
Sept. 6	18+	25	Grain	18.76	3.90	14.86	20.79	79.21	1.92	.49	.51	.05	.13

[a] See subsequent data and discussion concerning effect of omitting roots.

[b] Stems and leaves include chaff from grain on this date.

TABLE III.—*Constituents of barley withdrawn from a silty clay loam soil (1c) in 1916*

Date.		Age from planting (in weeks).	Number of plants.	Description.	Nitrogen (grams per plant).	Nitrogen[a] as nitrate (parts per million of soil).[b]	Phosphorus (grams per plant).	Phosphorus[a] as phosphate (parts per million of soil).[b]	Potassium (K).		Calcium (Ca).		Magnesium (Mg).	
									Grams per plant.	Parts per million of soil.[b]	Grams per plant.	Parts per million of soil.[b]	Grams per plant.	Parts per million of soil.[b]
June	12	6	69	Entire, except roots	0. 0824	22. 36	0. 0111	2. 09	0. 1199	7. 35	0. 0104	0. 64	0. 0120	0. 74
	26	8	49	....do	. 1351	36. 67	. 0334	6. 28	. 3012	18. 47	. 0301	1. 85	. 0278	1. 71
July	10	10	42	....do	. 1097	29. 77	. 0357	6. 71	. 2264	13. 49	. 0306	1. 88	. 0322	1. 97
	24	12	29	....do	1229	33. 35	. 0394	7. 40	. 1949	11. 95	. 0359	2. 20	. 0404	2. 48
Aug.	7	14	28	....do	1317	35. 74	. 0443	8. 32	. 2017	12. 37	. 0326	2. 00	. 0384	2. 35
	21	16	38	....do	1414	38. 37	. 0561	10. 54	. 2479	15. 20	. 0428	2. 62	. 0440	2. 70
	28	17	87	....do	1439	39. 05	. 0569	10. 69	. 2397	14. 70	. 0368	2. 26	. 0433	2. 66
July	10	10	42	Stems and leaves	083	22. 53	. 0291	5. 47	. 2098	12. 86	. 0281	1. 72	. 0291	1. 78
	24	12	29	....do	0413	11. 21	. 0147	2. 76	. 1568	9. 62	. 0312	1. 91	. 0284	1. 74
Aug.	7	14	28	....do	0223	6. 05	. 0083	1. 56	. 1559	9. 56	. 0272	1. 67	. 0231	1. 42
	21	16	38	....do.[c]	. 0317	8. 60	. 0176	3. 31	. 2078	12. 74	. 0387	2. 37	. 0317	1. 94
	28	17	87	....do.[c]	. 0279	7. 57	. 0151	2. 84	. 2022	12. 40	. 0325	1. 99	. 0279	1. 71
July	10	10	42	Heads	. 0267	7. 25	. 0066	1. 24	. 0166	1. 02	. 0025	. 15	. 0031	. 19
	24	12	29	....do	. 0816	22. 15	. 0247	4. 64	. 0381	2. 34	. 0047	. 29	. 0120	. 74
Aug.	7	14	28	....do	. 1094	29. 69	. 0360	6. 77	. 0458	2. 81	. 0054	. 33	. 0153	. 94
	21	16	38	Grain	. 1097	29. 77	. 0385	7. 24	. 0401	2. 46	. 0041	. 25	. 0123	. 75
	28	17	87	....do	. 1160	31. 49	. 0418	7. 85	. 0375	2. 30	. 0043	. 26	. 0154	. 94

[a] Nitrogen and phosphorus are here computed in terms of nitrate (NO_3) and phosphate (PO_4) for the purpose of making clearer the subsequent comparisons between plant withdrawals and the nitrate and phosphate of the soil as determined by water extraction.

[b] Computation of parts per million is based on the number of grams per plant and a unit container of 50 plants and 1,800 pounds of soil.

Grams per plant, times 61.23 $\left[\frac{50}{1,800 \times 453} \times 1,000,000\right]$ = parts per million.

[c] Stems and leaves include chaff from grain on this date.

TABLE IV.—*Constituents of barley withdrawn from a sandy loam soil (15) in 1917*

Date.		Age from planting (in weeks).	Number of plants.	Description.	Nitrogen (grams per plant).	Nitrogen[a] as nitrate (parts per million of soil).[b]	Phosphorus (grams per plant).	Phosphorus[a] as phosphate (parts per million of soil).[b]	Potassium (K).		Calcium (Ca).		Magnesium (Mg).	
									Grams per plant.	Parts per million of soil.[b]	Grams per plant.	Parts per million of soil.[b]	Grams per plant.	Parts per million of soil.[b]
May	21	3	97	Entire, except roots	0.0047	1.351	0.0006	0.1194	0.0047	0.3052	0.0007	0.0454	0.0007	0.0454
June	4	5	49	do	.0426	12.25	.0047	.935	.0461	2.993	.0060	.3896	.0036	.2337
	18	7	50	do	.1340	38.52	.0225	4.477	.1996	12.96	.0242	1.571	.0168	1.091
July	2	9	49	do	.3044	87.50	.0414	8.237	.4132	26.83	.0618	4.012	.0365	2.37
	16	11	25	do	.1899	54.60	.0489	9.730	.2744	17.82	.0530	3.441	.0313	2.032
	30	13	25	do	.2423	69.66	.0696	13.85	.3201	20.78	.0781	5.071	.0380	2.467
Aug	13	15	23	do	.3569	102.60	.0894	17.79	.4430	28.76	.1066	6.922	.0646	4.195
Sept.	6	18+	25	do	.3581	102.95	.0903	17.97	.3584	23.27	.0905	5.876	.0528	3.428
July	2	9	49	Stems and leaves	.2907	83.57	.0388	7.72	.4027	26.15	.0610	3.96	.0355	2.305
	16	11	25	do	.1403	40.34	.0392	7.80	.2430	15.78	.0483	3.136	.0272	1.766
	30	13	25	do	.1160	33.35	.0380	7.56	.2587	16.80	.0685	4.447	.0266	1.727
Aug	13	15	23	do	.1016	29.21	.0259	5.15	.3675	23.86	.0930	6.038	.0389	2.526
Sept.	6	18+	25	do[c]	.0728	20.93	.0175	3.48	.2826	18.35	.0831	5.396	.0335	2.175
July	2	9	49	Heads	.0137	3.93	.0026	.517	.0105	.682	.0008	.0519	.0010	.0649
	16	11	25	do	.0496	14.26	.0097	1.93	.0314	2.039	.0047	.3052	.0041	.2662
	30	13	25	do	.1263	36.31	.0316	6.288	.0614	3.986	.0096	.6233	.0114	.7402
Aug.	13	15	23	do	.2553	73.40	.0635	12.63	.0755	4.902	.0136	.883	.0257	1.669
Sept.	6	18+	25	Grain	.2853	82.02	.0728	14.48	.0758	4.922	.0074	.480	.0193	1.253

[a] Nitrogen and phosphorus are here computed in terms of nitrate (NO_3) and phosphate (PO_4) for the purpose of making clearer the subsequent comparisons between plant withdrawals and the nitrate and phosphate of the soil as determined by water extraction.

[b] Computation of parts per million is based on the number of grams per plant and a unit container of 50 plants and 1,700 pounds of soil.

Grams per plant, times 64.93 $\left[\frac{50}{1{,}700 \times 453} \times 1{,}000{,}000\right]$ = parts per million.

[c] Stems and leaves include chaff from grain on this date.

GROWTH PERIODS.—If we refer now to figures 1 and 2, it appears that growth may be divided into three periods: a preliminary period of eight to nine weeks from planting (five to six weeks from germination)

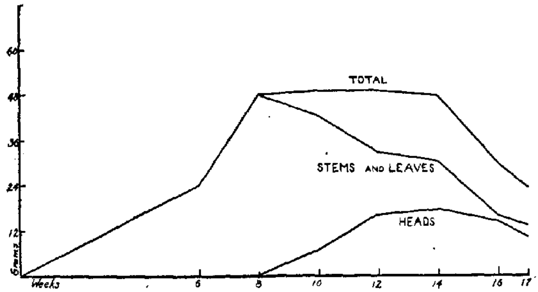

FIG. 1.—Growth reached by barley at different periods of cutting. Experiment of 1916.

in which the greatest gain in weight of the plant takes place; a second period of about six weeks, when the rate of gain in total weight falls off noticeably and in the 1916 experiment becomes negligible (it is during this period that the heads are formed and developed); and a

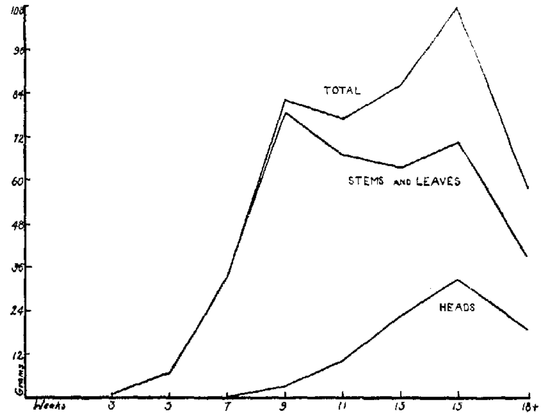

FIG. 2.—Growth reached by barley at different periods of cutting. Experiment of 1917.

third period of about three weeks, in which there is an absolute loss in weight not only in the plants as a whole but in the various parts, as is shown in both experiments. The first period is one of intense vegetative

activity; the leaves are a vivid green; the tissues are moist; and growth, measured in both weight and height, is considerable. The second period is clearly one of a different kind of activity; structural differentiation is taking place; and fully formed heads may be developed without any further increase in the growth of the plant, as is shown in the 1916 experiment when there was practically no increase in fresh weight after the eighth week. The leaves lose their green and moist appearance and the stems and leaves fall off in total weight whether that of the entire plant is increasing or not. The third period, again, is obviously different and is characterized by a loss of weight and by desiccation of all parts of the plant, accompanied by a more or less complete loss of the green color of actively growing plant tissue.

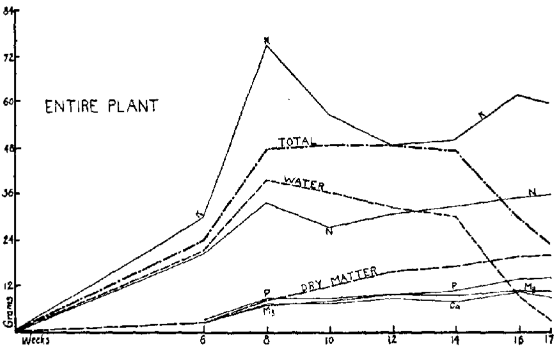

FIG. 3.—Relation of growth of barley to absorption of potassium, nitrogen, phosphate, calcium, and magnesium, for entire plant except roots. To emphasize the comparative differences in absorption of these elements, the quantities actually found have been multiplied by 250. Experiment of 1916.

When we consider the composition of the plant as represented by the dry matter and water content (fig. 3, 4) no very obvious relation is observed between the dry matter and the growth periods referred to heretofore; the variation in water content is, however, quite consistent therewith. This follows naturally enough from the fact that water constitutes such a large proportion of the plant up to the last four weeks of growth. The increase in the dry-matter content of the plant is represented by a fairly straight line, the only considerable break being in the plants from the more productive soil near the end of the season when there was an absolute loss.

The water content shows considerable variations, indicated by very sharp breaks in the lines at the beginning and end of the second growth period. The first of these breaks appears to be particularly significant because the soils were being maintained at that time at constant

(optimum) water content. This loss of water points to abrupt changes in the character of the internal activities of the plant, in complete accord with the vegetative changes to which attention has been called.

ABSORPTION BY THE PLANT.—(Fig. 3–8.) The expedient we have adopted of plotting the various elements on an enlarged scale brings out important differences in their behavior. Potassium and nitrogen, both in magnitude and in rate of absorption by the plant at all stages, are more nearly proportional to the total growth and water content of the plant than to that of the dry matter, while the reverse is true of calcium, magnesium, and phosphorus.

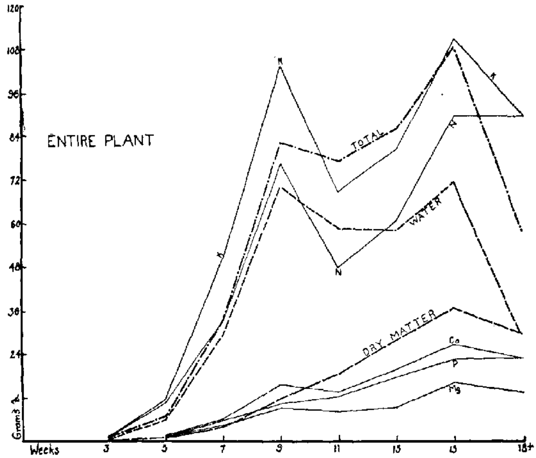

FIG. 4.—Relation of growth of barley to absorption of potassium, nitrogen, phosphate, calcium, and magnesium, for entire plant except roots. To emphasize the comparative differences in absorption of these elements, the quantities actually found have been multiplied by 250. Experiment of 1917.

During the first period of growth, ending eight and nine weeks from planting, the increase of potassium and nitrogen appears to conform very closely to the gain in total weight and water content of the plant. At the inception of the second growth period the interesting fact is developed that both of these elements diminish, apparently indicating a movement from the plant to the soil.

The increase of calcium, magnesium, and phosphorus closely parallels the formation of dry matter in both experiments up to eight and nine weeks, respectively, after which these elements lag behind. In the 1917 experiment a slight loss of calcium appears to take place between the ninth and eleventh weeks. The variation of the calcium in the

1916 experiment and of magnesium in both experiments at this same stage of growth is so small as to be within the experimental error of the

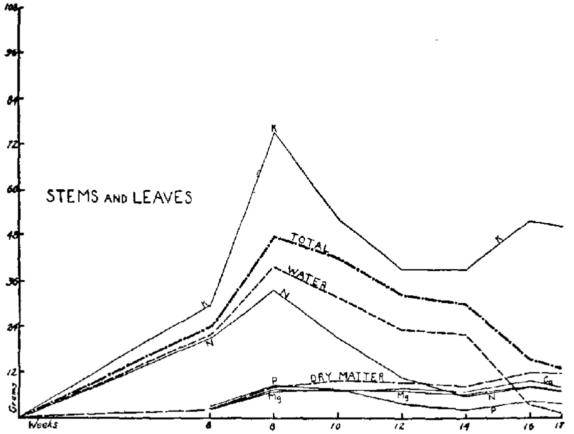

FIG. 5.—Relation of growth of barley to absorption of potassium, nitrogen, phosphate, calcium, and magnesium, for stems and leaves. To emphasize the comparative differences in absorption of these elements, the quantities actually found have been multiplied by 250. Experiment of 1916.

determination. It is quite possible, however, that the same causes that bring about such substantial losses of potassium and nitrogen at this time and appear to affect calcium, which has such different functions in plant metabolism, may not be without effect on the other elements. When the absolute losses noted above were first observed in 1916, we were inclined to doubt the accuracy of our data; but the 1917 experiment confirmed the observation in a most striking and convincing manner.

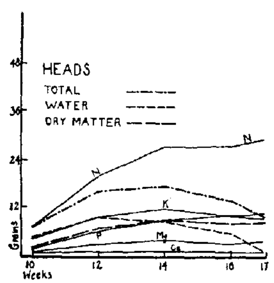

FIG. 6.—Relation of growth of barley to absorption of potassium, nitrogen, phosphate, calcium, and magnesium, for heads. To emphasize the comparative differences in absorption of these elements, the quantities actually found have been multiplied by 250. Experiment of 1916.

LOSSES OF SOIL CONSTITUENTS FROM THE PLANT.—The losses observed were not mechanical losses in decayed leaves (7), since they occurred at a period before there was any considerable drying out of the plant; furthermore the losses of fragments of vegetative tissue were negligible at all times under the conditions of the experiments. Losses from leach-

ing of the leaves, such as those suggested by LeClerc and Breazeale (*6*) and others, were rendered impossible by the protection of the plants

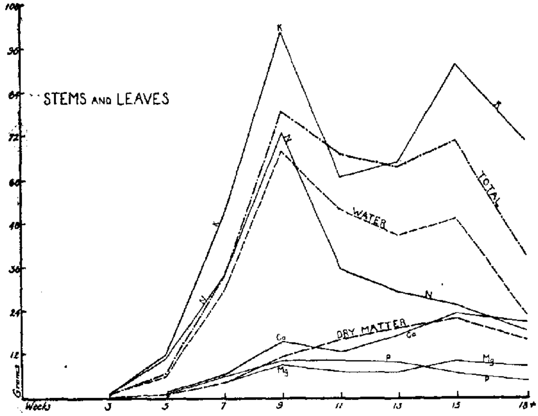

FIG. 7.—Relation of growth of barley to absorption of potassium, nitrogen, phosphate, calcium, and magnesium, for stems and leaves. To emphasize the comparative differences in absorption of these elements, the quantities actually found have been multiplied by 250. Experiment of 1917.

from rain at all times. If we eliminate the rather remote possibility of losses of volatile nitrogen from the leaves, which seems all the more improbable since potassium could not be eliminated in that way, it would seem that the constituents lost either became localized in the roots or returned to the soil. Either condition would represent a very important phenomenon; but migration of potassium and nitrogen from the plant into the soil is such a complete reversal of the ordinary condition that it must be in obedience to causative changes of considerable magnitude, which may be capable of measurement and if so would presumably shed light on the nutritional relations of plants and soils.

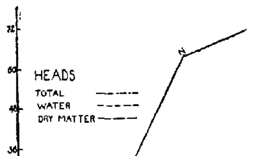

FIG. 8.—Relation of growth of barley to absorption of potassium, nitrogen, phosphate, calcium, and magnesium, for heads. To emphasize the comparative differences in absorption of these elements, the quantities actually found have been multiplied by 250. Experiments of 1917.

The data we have presented above are conclusive only of losses of nitrogen and potassium from the part of the plant growing above ground, inasmuch as we did not include the roots in our study.

We have explained heretofore our reasons for omitting a study of the roots of plants growing in natural soils. For the same reasons we have little confidence in the exactness of the findings of other investigators from similar experiments. It is interesting to note, however, that computations from the well-known work of Wilfarth, Römer, and Wimmer (9) show that of the elements in question not more than 10 per cent of the total nitrogen absorbed was contained in the roots at any stage of growth, and only 3 per cent of the total potassium. Data from the same authors, including the roots and stubble with stems to a height of 5 cm. above the surface of the soil, show a maximum of 22 per cent of the total nitrogen and 18 per cent of the total potassium at what appears to be about the same stage of development as our plants when the observed losses took place. Data obtained in this laboratory (3) from the same strain of barley grown in sand cultures at a little later stage of growth showed the roots to contain 9.6 per cent of the total nitrogen and 7.3 per cent of the total potassium content of the plant. In our experiment in 1917 the proportions of the total nitrogen and potassium lost from the upper part of the plant, including all of the stems and most of the stubble (see method of cutting described on page 53), were 38 and 34 per cent, respectively.

The magnitude of these losses as compared with the amounts of the elements found in the roots in the cases cited seems sufficiently great to justify the opinion that there is an actual movement of potassium and nitrogen from the plant into the soil at this stage of development. The losses, it will be observed, occur at the time the heads are beginning to form and to draw upon the remainder of the plant for these same constituents (fig. 5–8). There is evidently a concurrent migration of important constituents from the stems and leaves in two directions into the heads and into or through the roots into the soil.

The losses to which we have called attention are not to be confounded with those which apparently take place in numerous plants at the extreme end of the growing season. Here the losses occurred comparatively early in the growth cycle of the plant and were by no means final, being followed by appreciable gains in 1916 and by very substantial increases in 1917. However, the other kind of loss is also to be noted here, there being appreciable losses of potassium, calcium, and magnesium after the fifteenth week when the grain was ripening, in the 1917 experiment, and some indications of the same sort of thing in the work of the preceding year.

The experiments reported by Wilfarth, Römer, and Wimmer (9) show evidence of similar losses of potassium and nitrogen and also sodium, at what appears to be about the same early stage [1] of development of

[1] An exact comparison of the two studies is not possible because of differences of soil and climate. In the work quoted, the intervals between cuttings were so much greater (about four weeks as against two weeks) that a closer analogy may have been obscured.

both barley and wheat. The losses noted by them were, however, in every instance final and not succeeded by a further period of absorption as in our experiments.

The behavior of maize as reported by Hornberger (*4*) presents some very interesting analogies to the facts brought out in the present work. It is true that the author quoted shows no absolute losses of constituents derived from the soil prior to the ripening stage. He does show, however, that immediately after the period of maximum absorption and when the heads are beginning to form there is an abrupt slowing down of the rate of absorption of practically all elements. This again is followed by a period of rapid absorption, which in turn is succeeded by the ripening period in which there are absolute losses of all constituents except phosphorus.

Jones and Huston (*5*), also working with maize, showed a period of very rapid absorption of potassium at the eighth week from germination, just prior to the beginning of head formation, followed by a long period of slow absorption, succeeded in turn by a rapid absorption during the sixteenth week, and finally by an absolute loss in the seventeenth. The peak absorptions for nitrogen in the same plants were during the eighth and sixteenth weeks, with an intermediate period of decreased absorption.

On the contrary, the field experiments of Wilfarth, Römer, and Wimmer (*9*) show no losses of potassium and nitrogen at any stage in the growth of potatoes nor very striking changes in the rate of absorption of these elements.

The behavior of maize and barley as contrasted with that of potatoes would seem to indicate that the tendency toward a materially delayed rate of absorption, or absolute loss of constituents at an early stage of development, is probably a characteristic of types of plants whose growth cycle includes a period of extreme differentiation in constructive metabolism. We may, for instance, expect to find such a tendency in other cereal crops and in fruit trees at the period of fruit formation. On the other hand, the discrepancies in the behavior of barley, as shown by important differences of our results from those of Wilfarth, Römer, and Wimmer, indicate that other factors also have an important influence.

SOIL RELATIONS

The abrupt change in the water content and the loss of certain soil constituents from the barley plant at the height of the growing season have no very obvious relation to concurrent changes in external conditions. We can hardly conceive, however, that changes of this kind and magnitude are conditioned entirely by the specific peculiarities of the plants in which they are observed, even though they are not to be found in other types. It is pertinent to inquire more particularly, therefore, into the condition of the soil at the time these important changes take

place. For this purpose we present the data on the periodic water extractions (1 part of soil to 5 parts of water by weight) of the soil of the 1917 experiment.

TABLE V.—*Water extractions of fine sandy loam soil (15)*

[Expressed as parts per million of soil]

Date.	Weeks from planting crop.	Total solutes.		Potassium (K).		Calcium (Ca).		Magnesium (Mg).		Nitrate (NO_3).		Phosphate (PO_4).	
		Cropped.	Uncropped.	Cropped.	Uncropped.	Cropped.	Uncropped.	Cropped.	Uncropped.	Cropped.	Uncropped.	Cropped.	Uncropped.
Apr. 30	0	246	273	22.9	22.6	35.2	40.6	4.1	4.6	53.3	54.5	7.6	7.0
May 14	2	336	371	30.1	27.7	38.3	38.3	8.3	8.2	69.6	67.7	4.7	5.9
21	3	320	353	27.9	30.0	29.6	32.3	20.8	22.3	65.2	63.5	7.1	5.3
June 4	5	247	292	25.3	25.7	23.5	38.0	9.4	11.7	56.4	61.9	5.9	5.8
18	7	178	290	21.2	24.4	17.2	29.0	6.9	13.3	5.7	60.3	4.6	5.8
July 2	9	131	268	14.3	25.1	13.1	25.7	1.7	4.7	8.6	71.1	5.1	7.6
16	11	172	261	15.4	19.0	13.7	19.6	1.8	4.7	2.4	45.7	3.0	4.7
30	13	151	244	22.7	27.4	18.0	30.0	1.2	3.6	4.7	39.9	4.1	6.0
Aug. 13	15	134	224	26.8	31.8	15.7	20.6	2.2	4.1	2.8	37.1	7.8	10.6
27	17	138	277	21.9	33.0	20.2	20.6	2.9	7.1	5.2	77.7	2.3	6.5
Oct. 22	25	222	265	32.8	31.1	30.6	40.3	7.8	12.1	35.0	64.5	8.3	8.1

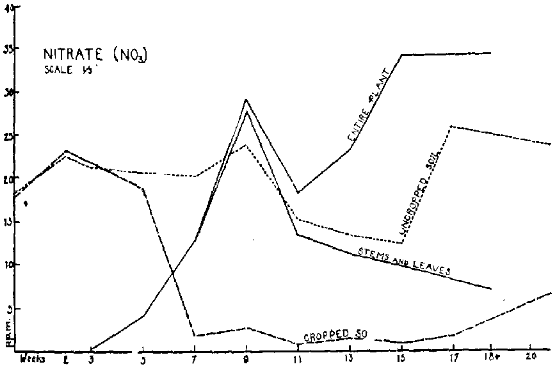

FIG. 9.—Absorption of nitrogen by barley, expressed as the nitrate (NO_3) equivalent and computed to parts per million of soil.

In order to bring out more clearly certain apparent relations between the water extracts and the amounts of soil solutes taken up by the plant, we have computed the plant constituents in terms of the corresponding ions of the soil and expressed these in terms of parts per million of the mass of soil upon which the plants were grown and in which the various constituents must have originated. The data from the soils are expressed in similar terms (fig. 9–13). It should be pointed out at once that the soil data are not to be too literally interpreted. For instance, it is clear that we can not expect that the gains and losses of a given con-

stituent by the plant will be accompanied by exactly equal losses or gains in the soil extract. The more obvious reasons for this are that the water extract is to be regarded only as an indicator of the general magnitudes of

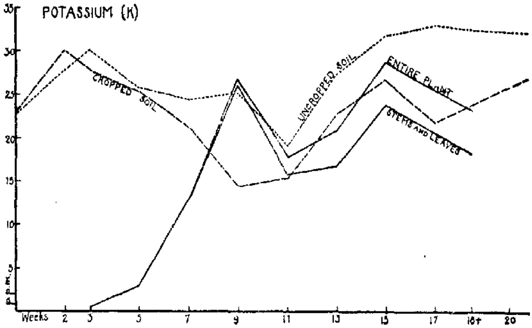

FIG. 10.—Absorption of potassium by barley, computed to parts per million of soil.

the solutes present and not as the equivalent of the soil solution, that ions absorbed by the plants may be partially or entirely replaced in the water extract by solution from the soil minerals, and that solutes lost from the plants may not reappear in the form determined in the soil extract.

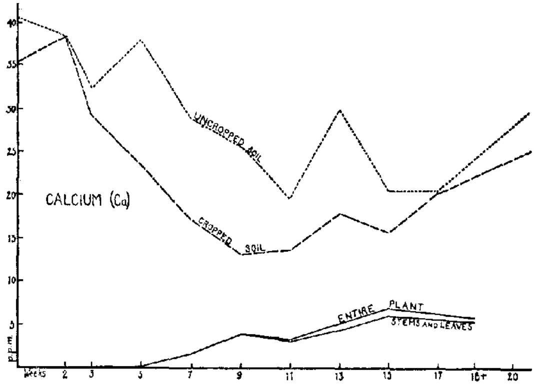

FIG. 11.—Absorption of calcium by barley, computed to parts per million of soil.

NITROGEN ABSORPTION.—(Fig. 9.) The maximum absorption of nitrogen took place between the third week from planting (time of germination) and the ninth week from planting. Almost the entire amount of

nitrogen absorbed could have been supplied by the nitrate in the soil at germination. The additional quantity necessary was presumably supplied by nitrification.

The nitrates in the soil approached a very low level at seven weeks and remained low for the rest of the season. We have repeatedly found such a

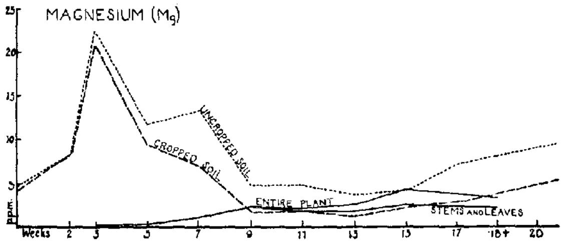

FIG. 12.—Absorption of magnesium by barley, computed to parts per million of soil.

drop to take place in numerous other cropped soils a few weeks after planting. The greatest rate of absorption by the plant occurred between the seventh and ninth weeks.[1] During the succeeding period, ninth to eleventh weeks, the loss of nitrogen from the plant took place. The conjunction of a low nitrate concentration in the soil and high nitrogen content of the plant,[2] soon followed by a movement of nitrogen from the plant toward the soil, is difficult to dissociate, although the exact

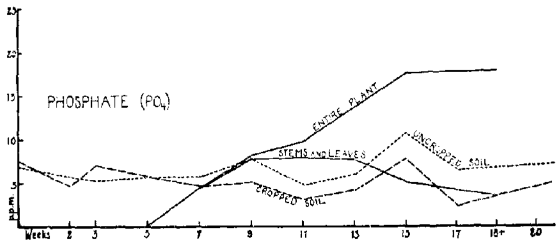

FIG. 13.—Absorption of phosphorus by barley, expressed as the phosphate (PO_4) equivalent and computed to parts per million of soil.

relation is not clear. A further and considerable absorption of nitrogen took place between the eleventh and fifteenth weeks. The rate of absorption, however, was never again so great as that of the period between the

[1] Nitrates, as such, were found in the plants in decreasing quantities up to nine weeks from planting.

[2] Determinations of the various forms of soluble nitrogen in the fresh plant substance at this stage would doubtless give interesting data in connection with the point under discussion here but were not feasible under the conditions of these experiments.

seventh and ninth weeks, and in spite of a continued low nitrate concentration we observe no further loss of nitrogen from the plant. The small additional increment of nitrogen subsequently absorbed, above that present at nine weeks, may be accounted for by concurrent nitrification during the 6-week period between the ninth and fifteenth weeks. The fact that the uncropped soil shows a loss of nitrate at this time is no evidence against such an assumption, inasmuch as nitrification may have been more intense in the cropped soil of low nitrate concentration.

POTASSIUM.—(Fig. 10.) As with nitrate, we observe here a lowered concentration of the soil extract coincident with a high rate of absorption by the plant and shortly afterward followed by a loss of the element from the plant. A little later potassium is again taken up by the plant at a period when the water-extractable potassium of the soil is increasing. If a loss of water-extractable potassium indicates a lowered concentration of the soil solution, some disturbance of the equilibrium between the latter and the cell sap must occur. Increased concentrations of potassium compounds with diosmotic properties in the cell sap would tend still further to change the previously existing equilibria and, if sufficiently great, account for a movement of potassium from the plant to the soil.

CALCIUM AND MAGNESIUM.—(Figs. 11, 12.) The small magnitudes involved in the fluctuations of these elements within the plant vitiate any definite conclusions therefrom. It is interesting to note, however, that there is a distinct loss of calcium and an apparent loss of magnesium between the ninth and eleventh weeks, the period immediately following a lowered concentration of the corresponding ions in the water extracts.

PHOSPHORUS.—(Fig. 13.) The water-soluble phosphorus of the soil seldom shows the considerable fluctuations observed in other elements concurrently with changes in the depression of the freezing point or with changes of soil conditions suggestive of corresponding changes in the soil solution. We can, therefore, hardly expect that the water-extractable phosphorus will shed much light on the mechanism of the process by which plants gain or lose very small increments of this constituent. We may, however, point out that the data have the minor merit of not being inconsistent with the suggestion made in connection with other constituents, in that phosphorus is the only element which appears to increase between the ninth and eleventh weeks and the only one in which the corresponding ion of the water extract does not decrease materially just before this period.

CONCLUSIONS

The absorption of certain soil constituents by barley is characterized by three distinct phases, coextensive with the more important stages of vegetative development. The first of these covers a period of progressively increasing rate of absorption, ending about the time the heads begin to form. At this time the absolute amounts of potassium and nitrogen

contained in the plant approach the magnitudes present at complete maturity. The potassium content may even be greater than at maturity. The beginning of the second phase is indicated not merely by a decreased rate of absorption as in maize but by definite and substantial losses of certain consitutients (notably potassium and nitrogen and apparently calcium) from the portion of the plant growing above the ground, and presumably from the entire plant. This loss takes place concurrently with the migration of the same constituents into the developing heads. The end of the second phase is characterized by a tendency to absorb again the soil constituents previously lost. This tendency may result in taking up considerable quantities when the plants are very large and well developed, as in the 1917 experiment. The third phase, occurring at the time of ripening of the grain, is marked by a practically complete cessation of absorption of all constituents and an actual loss of most of these.

The more significant facts brought out here would appear to be: That the two elements with which plant growth in general is most closely associated may approach or exceed their maxima at a comparatively early stage of the plant's development—that is, at the beginning of head formation; that absorption of potassium and nitrogen during the first period of growth is approximately proportional to the growth attained, and in the succeeding periods the final dry-matter content of the crop more than doubles without any very substantial increase in nitrogen content and with an actual loss of potassium; furthermore, that the final dry-matter content of the crop, even when it varies as much in yield as in the cases reported, appears to be nearly proportional to the fresh weight of the crop at the end of the first period. A direct relation is thus traced between the amount of dry matter in the final yield and the amounts of potassium and nitrogen absorbed in the first stage.

The fact that nitrogen and potassium tend to leave the plant just after the heads begin to form does not prove that their presence is inimical to head formation (no actual losses occur in maize, for example), but indicates rather that continued absorption at this stage is probably incompatible with normal development.

The explanation of the mechanism by which losses of certain constituents take place from growing plants at an early stage of growth must await further detailed studies and a considerable advance in our knowledge of plant metabolism and particularly of the forms in which the various elements exist in the cell sap during the period of translocation to the heads. We shall content ourselves here with the suggestion that such losses are probably due to complex but purely physical causes, a suggestion rendered plausible by the simultaneous occurrence of low concentrations of the water extracts and the movement of mobile constituents from the leaves to the heads.

The concentration of the water extracts of normal soils under crop and producing good yields varies greatly during the growing season (*8*). With barley and numerous other plants such concentrations may become relatively low after the plant becomes well established. Nitrates in particular tend toward a very low level in cropped soils at the height of the growing season even if present in considerable quantities at the time of planting the crop. Since the variation of the freezing-point depressions appears to accord closely with the water extracts (*2*), it seems clear that the normal habitat of annual land plants includes a soil solution which may be of relatively high concentration at the beginning of the growing season but which inevitably falls off at a certain stage of development if the growth is at all prolific. In the light of the results reported above, this diminution of total and nitrate concentration, which we believe to be general in cropped soils, doubtless has an important and probably a favorable effect on crop production. This is confirmed with respect to nitrogen by the abundant evidence we have that applications of nitrates late in the season delay the maturation of grain crops. We interpret these facts to mean that the mutual relations of soils and plants are such that it is generally desirable to have the large amounts of solutes incidental to relatively high concentrations in the soil solution at the commencement of the plant's growth cycle but that it is unnecessary and may be undesirable to maintain this condition during certain later stages of growth. This conclusion has been successfully utilized in this laboratory (*3*) in formulating water-culture experiments with barley, but may not apply to all crops.

It would seem that studies of the absorption of other plants grown on natural soils, particularly those yielding good crops, have important applications in investigations for determining the conditions for optimum growth by means of sand and water cultures; for while the amount of a given constituent absorbed does not necessarily indicate the quantity essential to proper development, fluctuations in the rate of absorption may be expected to reflect the nutritional peculiarities of the crop and serve as a guide in regulating the concentrations and amounts of solutes at successive stages of growth.

SUMMARY

(1) The composition of barley grown on two different soils was studied at successive stages of growth.

(2) In spite of differences in the character of the soils and the yields obtained, a striking similarity was observed in the growth cycles and in the successive changes in the rates of absorption of the plants.

(3) Attention is called to remarkable losses of potassium and nitrogen from the plant at an early stage of development, which are succeeded by renewed absorption at a later period.

(4) The losses observed occurred when the constituents of the water extracts of the soil were at or approaching their minima and when these same constituents were moving from the leaves to the heads.

(5) The suggestion is offered that for many plants high concentrations of the soil solution at certain stages of growth are probably not necessary and may be undesirable.

(6) A plea is made for further studies of other types of plant by the methods used herein, to obtain data for the more rational formulation of experiments with sand and water cultures.

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RELATION OF THE CONCENTRATION AND REACTION OF THE NUTRIENT MEDIUM TO THE GROWTH AND ABSORPTION OF THE PLANT

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INTRODUCTION

The investigation of the growth of plants from the standpoint of the agricultural chemist involves the study of both the soil and the plant. Until recently far greater attention has been given to the chemistry of the soil than to the nutrition of the plant, yet it is obvious that any satisfactory understanding of crop production is concerned as indispensably with the metabolism of the plant as with the chemical reactions of the soil. It is essential to learn what the plant absorbs and metabolizes as well as what the soil solution contains. Of fundamental importance to either phase of the problem is the recognition of the dynamic nature of both the plant and soil systems. Nearly all the studies of the past in soil chemistry have been concerned with the soil as a static system, and thus we have recorded countless experiments dealing with the total composition, hydrochloric acid extracts, lime requirements, and other gross characteristics of the soil. C. B. Lipman (*23*)[2] has pointed out the great service performed by Cameron in introducing certain physico-chemical considerations into soil studies, even though the neglect of some of the modifying factors led to conclusions at variance with the true state of affairs.

Recent researches recognize the paramount importance of the soil solution as the medium from which plants derive their inorganic nutriment. As a result various attempts have been made to obtain some definite conception of the concentration and composition of the actual soil solution by such methods as those proposed by Morgan (*31*) and C. B. Lipman (*22*). A very great advance in this direction has been made by Bouyoucos and McCool (*3*) in their application of the freezing-point method to the study of soil phenomena.

About four years ago this laboratory became engaged in an extensive research on the water extracts of soils held under conditions of exceptional control (*42*). The freezing-point method just mentioned was used also in determining actual osmotic pressures in the soil solution (*17*). The results from both methods of investigation, reinforced by many

[1] With the cooperation of F. W. Weitz. Acknowledgment is made also of the careful analytical work performed by J. C. Martin and A. W. Christie of this laboratory.

[2] Reference is made by number (italic) to literature cited, p. 114-117.

supplementary studies later, have shown very clearly that the soil solution is never in a state of final equilibrium but on the contrary fluctuates daily and seasonally and is profoundly modified as a result of absorption by the plant in such manner that during certain periods the concentration of the soil solution may be reduced to a very low level. Further work by Bouyoucos and McCool (*4*) recently has confirmed these absolutely essential principles.

Along with the concentration and composition of the soil solution, the reaction, or hydrogen-ion concentration, is a definite chemical factor, which under certain circumstances may become of importance through its modifying influence on the soil solution and on absorption by the plant. Previous work by Gillespie (*13*) and by Sharp and the author (*38*) has demonstrated the common existence of soils of distinctly acid reaction as shown by hydrogen electrode measurements. More recent studies by Gillespie and Hurst (*14*), Plummer (*33*), and Gainey (*11*) indicate that various important deductions relative to the soil solution may be drawn from the data obtained by these methods of investigations.

It has been deemed essential to present the foregoing introduction, since the experiments to be described in this paper have their basis in the theoretical considerations, experimental data, and methods resulting from the researches mentioned above, or others concerned with similar underlying principles. However small the beginning, it is hoped that the present studies in plant nutrition may have a special interest due to the use of the more recent methods of investigation and to the attempt made to correlate the results with such knowledge as we now have regarding the soil solution.

GENERAL METHODS OF EXPERIMENTATION

Since it is impossible to govern the exact concentration, reaction, and composition of the soil solution, any rigid control of nutrient solutions requires the use of water and sand cultures. These methods have been employed since the beginnings of the scientific study of agriculture, yet it is only recently that any systematic attempt has been made to elucidate by their use the fundamental problems of plant nutrition aside from the determination of the elements essential for growth long since established in the literature of plant physiology. Even at the present time the control of conditions is very incomplete. Somewhat surprising is the general absence of chemical control as exercised in the analyses of nutrient solutions or of the plants produced. The actual absorption under varying conditions has seldom been studied on any sufficient scale with plants grown for an extended period, although there may be a few exceptions to this statement, as in the recent work by Waynick (*52*) on antagonism and of Schreiner and Skinner (*37*), who have made a large number of analyses of solutions in which wheat seedlings had grown. The question

of absorption, as will be made evident later, involves the whole technic of solution-culture experimentation in its relation to the size of culture vessels and frequency of renewal of solutions, while the interpretation of the data likewise must take into consideration the nature and extent of absorption.

In all of the present experiments a selected Beldi variety of barley was used as the test plant. Although the conclusions of this article are based on experiments with barley, it is our opinion that the general principles of nutrition and absorption deduced apply as well to at least most of the common plants of agricultural interest. Germination was accomplished very conveniently by Waynick's (*52*) method. The bottles for the solution cultures were coated on the outside with black paint and then wrapped with white glazed paper. The latter precaution is very necessary when the cultures are exposed to strong sunlight, on account of heat absorption. Wedges, slightly truncated, were cut from the cork stoppers, and the seedlings were fixed in the openings by means of cotton. As the plants grew and tillered, the size of the openings was increased from time to time by cutting off further segments from the wedge. This part of the technic is important, since there should be no mechanical restriction to the development of the plant. In fact it may be stated as a general principle that the technic employed should place no limitation on the growth of the plant other than that caused by the variables under consideration.

Two sizes of bottles were used, of approximately 1,000- and 2,200-cc. capacity. In some experiments only one plant was placed in each bottle, in others two plants. Thus a relatively large volume of solution per plant was provided. The more detailed discussion of this point is reserved until later in the article. The volume of solution was maintained as constant as possible by the addition of distilled water daily or sometimes oftener.

In order to support the growing plants, glass rods were fixed in the corks and provided with loose loops made of cotton string. Great care was taken that there should be no crowding together of the leaves, for it is essential that each leaf receive the maximum light, and this would be impossible if the plants were bound tightly to the supporting rod. Most of the corks were dipped in melted paraffin previous to use. Any excess of paraffin is, however, to be avoided, since it may soften in the sunlight and injure the seedling at the point of contact.

In making up the nutrient solution the ordinary supply of distilled water was used. This had been in contact only with glass or block tin. At no time was there any evidence of toxicity due to the distilled water. Comparative tests, using water treated with "G Elf" carbon black as recommended by the Bureau of Soils, did not indicate any advantage in this treatment. Baker's analyzed chemicals were usually employed in making the nutrient solutions. Strong stock solutions of calcium nitrate

($Ca(NO_3)_2$), potassium nitrate (KNO_3), magnesium sulphate ($MgSO_4$), and potassium phosphate (KH_2PO_4 and K_2HPO_4) were made and diluted to the desired degree. The composition of the nutrient solutions was then determined by analysis.

In most investigations on plant nutrition, the question of the iron content of the nutrient solution has not received sufficient consideration. Gile and Carrero (*12*) have very thoroughly examined this matter and have reached the conclusion that in the absence of special precautions, it is often possible that the plant may be inhibited in its growth by an insufficient supply of available iron. Our experience is entirely in accord with this view. The presence of sufficient dissolved iron in the culture solution will depend upon the form and quantity of the iron salt used, upon the concentration and reaction of the solution, and upon the time of standing. By direct qualitative tests with potassium sulphocyanid (KCNS) it is easy to show that in certain cases no dissolved iron is found after a comparatively short time, even though considerable quantities of iron chlorid ($FeCl_3$), iron sulphate ($FeSO_4$), etc. had been added to the solution. The solubility is of course greater in solutions of higher hydrogen-ion concentration; but even in acid solutions, when the total concentration of phosphate (PO_4) is high, all the iron may be precipitated. Iron citrate and tartrate seem to be the most effective forms of iron to use. It is also desirable to add the iron solution or suspension to each culture bottle at the time the solution is changed. In any case there must be assurance that iron is not a limiting factor, as it might easily become in solutions of higher concentrations even when the more dilute solutions were plentifully supplied. The experience of Gile and Carrero (*12*) and actual tests with KCNS on the filtered solution would seem to make possible the necessary control.

METHODS USED IN SAND-CULTURE EXPERIMENTS

The method of sand culture has been extensively employed because such a medium obviously affords a more natural habitat for the plant roots than solution cultures can furnish. The selection of the sand is not a matter of indifference, although in many experiments beach sand has been used. This could scarcely be regarded as an entirely inert substance free of soluble material. For the present experiments "Ottawa" sand was selected. This sand is exceptionally pure. Analysis showed that it contained 99.8 per cent silica (SiO_2). In the latter series of experiments the sand received additional purification by treatment with hydrochloric acid (HCl) and subsequent washing with water. Unless the sand is treated with HCl it is possible that a trace of alkaline-reacting substance may alter the reaction of certain nutrient solutions. After the treatment described above, however, it has not been found that any significant change in reaction takes place as a result of contact with the

sand, at least for limited periods of time. The physical analysis of the sand was as follows:

	Per cent.
Passing 60-mesh sieve	60. 0
Passing 80-mesh sieve	26. 7
Passing 100-mesh sieve	9. 7
Passing 150-mesh sieve	2. 1
Passing 200-mesh sieve	. 8
Passing finer than 200-mesh sieve	. 6

The most valuable method of carrying out sand-culture experiments is that described by McCall (*26, 28, 29*). By this procedure it is possible to change the nutrient solution as desired. In our experiments large glazed earthenware jars with a capacity of 5 gallons were used with only four or five plants in each jar. It is possible in this way to grow plants without restriction of root development, which might not be possible in small jars. It was not found convenient to withdraw the solution through tubes placed in the bottom of the jars, so a siphon arrangement was finally adopted. A wide-bore glass tube was placed so that it extended to the bottom of the jar. The upper part was bent at right angles and connected through a receiving bottle to a Nelson suction pump. To prevent the sand from being carried over with the liquid a filter of two thicknesses of muslin cloth was fixed on the lower end of each glass tube and held in place by a tightly fitting rubber tube. The use of a little air pressure served to free the filter from any finely dissolved material which might tend to stop the flow of solution. When such arrangements are properly made, six jars simultaneously can be sucked free of all excess solution in a short period.

Water transpired or evaporated was replaced by the addition of distilled water, making up to original weight. The jars were moved about by means of a traveling pulley. One difficulty connected with the addition of water at the top is its tendency to wash down nutrients to the bottom of the jar so that the concentration of the solution is not uniform. In the final sand-culture experiments this has been largely overcome by the use of a glass percolator of 1-liter capacity inverted in the middle of the jar and not filled with sand. Most of the water was added through the projecting tube of the percolator and became equally distributed throughout the jar. In order to test the concentration of the solution, portions of sand were removed at various intervals and freezing-point lowerings determined.

METHODS OF CONTROL

Various methods of control were used during the investigation. These included determinations ot osmotic pressure by the freezing-point method both in solutions and when necessary in the soil or sand directly, described by Bouyoucos and McCool (*3*). For estimating hydrogen-ion con-

centration the colorimetric methods of Clark and Lubs (*8*) were employed, or, for estimating soils, direct measurements by means of the hydrogen electrode, in the manner described by Sharp and the author (*38*). Reactions have been calculated to the customary P_H values. Conductivity measurements were carried out in the usual way at a temperature of 25° C. For standardization of the electrode a *N/50* potassium chlorid (KCl) solution was used.

Since conductivity measurements express the total conducting power of the solution and are necessarily influenced by the nature of the ions, degree of dissociation, etc., they can be regarded as giving only approximate values, showing the general trend and magnitudes of absorption. For the latter purpose they are very convenient, and with the nutrient solutions and concentrations used in this experiment it has been found that the resistance varies with the concentration in a fairly direct ratio.

In many instances chemical analyses for calcium (Ca), magnesium (Mg), phosphate (PO_4), nitrate (NO_3), sulphate (SO_4), and potassium (K) have been made on the solutions or the plants. Whenever possible standard gravimetric and volumetric methods have been used. Occasionally, when very small concentrations were involved, the special technic described by Stewart(*42*) has been found valuable.

In the study of the absorption by the plant the culture jars were made up to the original weight with distilled water then thoroughly mixed by passing a current of air through, after which samples were taken for conductivity measurements or composites made for analysis. Before the jars were made up to weight the cork and plant were removed and temporarily placed in another jar. The roots were allowed to drain as thoroughly as possible, and since they were equally saturated with liquid at all times it is not probable that the general tendency of the results would be appreciably influenced by the loss of solution adhering to the surface of the roots. In several experiments conductivity measurements have been made on each individual jar in order to ascertain the degree of variability displayed by individual plants.

PRELIMINARY SAND CULTURES, SERIES I

Several years ago an attempt was made by the use of sand cultures to gain some idea of the effect of concentration of the nutrient solution on the growth of the barley plant. At this time arrangements were not available for changing solutions, and additional quantities of nutrient solution were added as water was lost by transpiration. Thus there was no control of exact concentrations as there was in the later experiments. It is thought worth while, however, to give these results a brief consideration, since they clearly indicate a definite relation between the nutrients present and the yield of grain and straw. In the critical discussion of other experiments these earlier data may be very helpful.

In this first series of sand-culture experiments 3-gallon jars were used, with seven plants in each jar. Nutrient solutions were added at the beginning to make a moisture content of about 14 to 15 per cent. Later, as transpiration occurred, more solution was added to each jar to make up for water lost. The total quantity of nutrient solution applied to each jar was approximately 5,000 cc. The composition of the nutrient solution was based on a general formula given in texts on plant physiology and was as follows:

	P. p. m.		P. p. m.
NO_3	163	Mg	34
K	85	Na	68
Ca	43	Cl	105
PO_4	163	SO_4	140

Concentrations were in the proportions of 200, 400, 800, and 1,600 parts per million of total salts. For each concentration 7 jars were used, with a total of 49 plants. The plants were cut when the grain was in the "hard dough" stage, and separation of heads and straw was made. The roots were recovered from the dried sand and freed as far as possible from adhering sand. Analyses were made on composite samples of the dried material, separating the plant into heads, straw, and roots. The determinations on the roots were calculated to a silica-free basis. In the following table are presented the data for yields in terms of dry weights, with percentages and total quantities of various elements.

TABLE I.—*Weight and composition of barley*

SAND CULTURES, SERIES 1

Part of plant analyzed.	Concentration of solution.	Average air-dry weight per plant.[a]	Composition (on water-free basis).					Total quantity absorbed per plant.				
			N.	K.	P.	Ca.	Mg.	N.	K.	P.	Ca.	Mg.
	P. p. m.	*Grams.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Stems and leaves	200	0.44	0.60	1.49	0.46	0.65	0.42	0.0026	0.0062	0.0019	0.0027	0.0018
	400	.96	.59	1.77	.54	.53	.28	.0055	.0163	.0050	.0049	.0026
	800	2.29	.61	2.18	.58	.50	.29	.0135	.0480	.0128	.0110	.0064
	1,600	5.00	.55	2.38	.57	.42	.25	.0270	.1170	.0280	.0205	.0125
Heads	200	.10	1.29	1.23	.45	.19	.20	.0012	.0011	.0004	.0002	.0002
	400	.31	1.24	.90	.44	.14	.23	.0037	.0027	.0013	.0004	.0007
	800	.91	1.41	.82	.42	.10	.18	.0123	.0071	.0036	.0009	.0015
	1,600	2.68	1.49	.94	.52	.07	.15	.0372	.0234	.0129	.0018	.0038
Roots[b]	200	.15	.65	1.47	.46	.19	.17	.0010	.0017	.0007	.0003	.0002
	400	.27	.65	1.20	.43	.21	.27	.0017	.0030	.0011	.0005	.0007
	800	.33	.74	1.23	.41	.34	.28	.0024	.0039	.0013	.0011	.0009
	1,600	.87	.80	1.29	.78	1.03	.13	.0068	.0110	.0066	.0087	.0011

[a] Barley grown in adjacent soil tanks at the same time gave from two to five times the yield from best sand culture.

[b] Calculations made on silica-free basis.

After the first few weeks very marked differences were noted in the appearance of the cultures, and with each successively higher concentration the growth was apparently nearly doubled. These general observations were corroborated by the final yields.

In this preliminary experiment the point to be emphasized is the direct relation of nutrients to yield of both grain and straw when either concentration or total supply is insufficient, and also the fact that the total quantities of Ca, K, Mg, PO_4, and N absorbed per plant vary directly with the concentration and total supply of the nutrient solution and in some cases are roughly proportional. The percentages on the basis of dry weight are, on the whole, not very dissimilar. In the heads the higher yielding plants show a lower percentage of some elements on account of the production of a better filled grain. In the straw the percentage of K increases with increasing concentrations.

It is of some interest to compare in each concentration the total quantities of important elements found in the crop with the total quantities added to the sand during the season. These figures are given in Table II.

TABLE II.—*Percentage of absorption of total nutrients added to jars* [a]

SAND CULTURES, SERIES I

Concentration of solution (in p. p. m.).	N.	K.	P.	Ca.	Mg.
200	55	45	24	30	27
400	72	64	35	33	29
800	82	75	36	32	28
1,600	103	96	49	39	27

[a] Calculations made on basis of total quantities contained in whole plants.

It will be observed that somewhat similar percentages of Ca and Mg were absorbed in each of the four different concentrations but that higher percentages of K, PO_4, and NO_3 were absorbed from the higher concentrations. In fact within the limits of error all of the K and NO_3 were utilized by the plant. When these data are later considered from a critical standpoint in connection with questions of supply and concentration, it will become evident that the data for absorption do not represent simply the influence of concentration. They may be interpreted to mean that in the lower concentrations the total supply was insufficient during the first part of the growth period, thus stunting the plant in such a way that later additions of nutrients could not be absorbed at a maximum rate, as they could be in the highest concentration. It should be stated finally that these sand cultures were placed out of doors in good light, adjacent to crops grown in a number of different soils at the same time. In all these soils the crop yields were much superior to those produced in the highest yielding sand culture. Limitations in the nutrient media of the sand cultures must therefore have existed and undoubtedly are to be ascribed to deficient total supply.

SAND CULTURES, SERIES 2

In any experiment similar to the one first described, it is clearly unjustifiable to interpret the results in terms of concentration or ionic ratios. Such an interpretation is warranted only when an opportunity is afforded for controlling the concentration of the solution at all times. In this second experiment the method of McCall (*26*) has been adopted, as previously stated. Solutions were changed during the period of active absorption every three days; and observations on the sand showed that the solutions were kept relatively constant, although on some occasions the leaching of nutrients to the bottom of the jar caused considerable fluctuations.

The plants were grown out of doors from August to December. There was abundant vegetative growth, but the temperature and light conditions did not permit the production of grain. The plants were still green when cut. We may use the data from this experiment, therefore, to indicate the general relation of concentration to yield in terms of dry weight of tops and roots and to the absorption of important elements while the plant is in an active state of metabolism.

The composition of the nutrient solution used in this and subsequent experiments had its basis in the analyses of water extracts of soils which had been under observation for several years, as described by Stewart (*42*). The nutrient solution was so constituted as to give approximately the same relations between the more important ions as that found in the water extracts of fertile soils at the period when the crop was actively absorbing. For the purposes of the present investigation this seemed as logical a basis as any for making up the nutrient solution. Possibly other combinations might give somewhat higher yields at times, but the ratios between the elements in the solutions employed were certainly not unfavorable. Moreover, within wide limits the broad relations of reaction and concentration to the course of absorption will not be affected by small differences in ionic ratios.

The nutrient solution of 0.78 atmospheres osmotic pressure had the following composition:

	P. p. m.
NO_3	700
K	284
PO_4	136
Ca	200
Mg	99
SO_4	368
NaCl	30

$P_H=6.8$.

The other concentrations used were 0.10, 0.25, 0.48, and 1.45 atmospheres.

The yields and analyses of plants are given in Table III.

TABLE III.—*Weight, composition, and total absorption per plant*

SAND CULTURES, SERIES 2

STEMS AND LEAVES

Concentration of solution.	Average air-dry weight per plant.[a]	Composition (on water-free basis). Total N.	Nitrate N.	Total P.	Water-soluble P.	Insoluble P.	Total K.	Water-soluble K.	Insoluble K.	Total Ca.	Water-soluble Ca.
Atmospheres.	*Grams.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*
0.10	6.2	2.65	0.02	0.72	0.62	0.10	3.97	3.44	0.53	1.00	0.85
.25	15.3	3.14	.14	.84	.66	.18	5.38	4.65	.73	1.21	.81
.48	24.0	3.85	.37	.95	.75	.20	6.90	6.10	.80	1.24	.77
.78	25.5	4.03	.46	.92	.77	.15	7.59	7.08	.51	1.09	.73
1.45	26.5	4.01	.52	.85	.71	.14	7.63	6.85	.78	.99	.70
[b]0.10 to .48	13.8	3.87	.51	.91	.67	.24	7.47	6.73	.74	1.27	.81
ROOTS											
0.10	1.30	2.35	....	0.48	....	....	....	....	....	0.49	....
.25	1.85	2.46	....	.60	0.31	0.29	....	2.75	....	.66	0.52
.48	2.95	3.61	0.30	.94	.41	.53	4.43	4.07	0.36	1.34	.60
.78	3.85	3.97	.50	1.45	.44	1.01	6.38	5.62	.76	2.67	.74
1.45	3.80	3.67	.69	2.42	.40	2.02	5.23	5.09	.14	4.42	.82
[b]0.10 to .48	2.10	4.03	....	.88	.48	.40	....	4.39	....	1.03	.94

STEMS AND LEAVES

Concentration of solution.	Average air-dry weight per plant.[a]	Composition—Continued. Insoluble Ca.	Total Mg.	Water-soluble Mg.	Insoluble Mg.	Total quantities absorbed. N.	P.	K.	Ca.	Mg.
Atmospheres.	*Grams.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
0.10	6.2	0.15	0.40	....	....	0.154	0.041	0.230	0.058	0.023
.25	15.3	.40	.43	0.41	0.02	.456	.122	.780	.176	.062
.48	24.0	.47	.44	.39	.05	.878	.216	1.570	.283	.100
.78	25.5	.36	.43	.36	.07	.988	.227	1.860	.267	.105
1.45	26.5	.29	.42	.42	.00	1.020	.215	1.935	.252	.107
[b]0.10 to .48	13.8	.46	.48	.42	.06	.506	.120	.978	.166	.063
ROOTS										
0.10	1.30	....	0.22	....	....	0.031	0.006	0.017	0.006	0.003
.25	1.85	0.14	.35	0.23	0.12	.045	.011	.049	.012	.007
.48	2.95	.74	.42	.36	.06	.106	.028	.130	.039	.012
.78	3.85	1.93	.62	.44	.18	.153	.056	.246	.103	.024
1.45	3.80	3.60	.71	.44	.27	.140	.092	.198	.169	.027
[b]0.10 to .48	2.10	.09	.62	.60	.02	.085	.018	.076	.022	.013

[a] Averages of 10 plants except in the 0.10 and 0.10 to 0.48 atmosphere concentrations, which were averages of 5 plants. Mean deviation per plant approximately ±2 gm., for tops.

[b] Cultures started with solution of 0.10 atmosphere concentration, after 52 days changed to 0.48 atmosphere.

The dry weights indicate that under these conditions a concentration of 0.10 atmospheres was too low, 0.25 atmospheres possibly sub-optimum, while no important difference between 0.48 atmospheres and 1.45 atmospheres was referable to the nutrient solutions. In other words, the optimum concentration—that is, the least concentration giving a maximum yield—would be found between 0.25 atmospheres and 0.48 atmos-

pheres. It is not certain, however, that the 0.10 atmospheres concentration was always constant, in spite of the great volume of solution used.

Especially interesting are the data showing in percentages the composition of the different parts of the plant. Some idea may be gained here of the influence of concentration on the absorption of individual elements and of the distribution between roots and tops. In the first place, the analyses of the tops show an increase of N from 2.65 per cent in the concentration of 0.10 atmospheres to a maximum of 4.03 per cent in the concentration of 0.78 atmospheres. Likewise the total K increases nearly 100 per cent. No such increase is noted, however, for PO_4, Ca, or Mg. The NO_3 also increases regularly with increasing concentration, and in the higher concentration about 0.5 per cent of nitrate nitrogen is found.

The elements soluble in cold water were determined by shaking the dried and ground sample with an excess of water, filtering, and then estimating the total quantity of each element found, the final calculation being based on the weight of dry material. The striking increase in percentage and total quantity of K in the tops of each plant is largely referable to K soluble in water. Most of the P and almost all of the Mg were soluble. Only about two-thirds of the Ca was soluble.

When we examine the data from analyses of the roots we meet with a different set of relations. There is an increasing percentage and total quantity of N and K, as in the tops; but, unlike the tops, the roots show very large increases in PO_4, Ca, and Mg. The partition between soluble and insoluble fractions shows that the increase is principally due to insoluble forms of the elements. The data suggest the hypothesis that with increasing concentration insoluble phosphates of Ca and Mg are precipitated in the roots, while the tops of the plants principally store excess N and K.

It should be repeated that in this experiment the large containers (5-gallon jars), together with frequent changes of solution, maintained, with the possible exception of the lowest concentration, an approximately constant concentration at the different levels. Thus the results indicate, at least in a general way, the influence of concentration rather than the limitation of insufficient total quantities. When such concentrations are maintained continuously, it is apparent that the plant may attain a condition in which the percentage of certain elements in its composition is very high, far higher than for plants grown under different conditions or in the field. It is of course understood in a general way that fertilization may affect the composition of the crop, but only in an experiment of the kind outlined above is it possible to point out definite and logical relationships. Also, it is practically impossible to obtain reliable results from the roots of plants except in sand and water cultures. It is not practicable to recover the roots from the soil quantitatively, and contamination is unavoidable. The results from this experiment are

therefore of interest in themselves and will also be pertinent to the further discussion of the course of absorption by the plant.

During the growth period of this series frequent observations were made on tillering and height. Except in the lowest concentration, heights were practically uniform. The number of tillers per plant, however, seemed to increase with increasing concentration. The total yield of dry matter per plant justifies the conclusion that under the conditions of experimentation here described there is no restriction on the optimum production of vegetative growth traceable to insufficient nutrients or limited size of containers.

SAND CULTURES, SERIES 3

During the following summer a further set of sand-culture experiments was carried out. The technic was similar to that of the preceding experiment except for the improved method of distributing the solution, described in the first part of the article. In this series sixteen 5-gallon jars were used with three concentrations of solution of 0.95, 1.95, and 3 atmospheres, respectively. The concentration of solution in four of the jars was decreased after 6 weeks from a concentration of 0.95 atmospheres to one of 0.15 atmospheres, in four other jars after 9 weeks, and in another set after 12 weeks. In the two highest initial concentrations a decrease was made after 6 weeks to 0.95 atmospheres concentration, and after 9 weeks to 0.15 atmospheres. The object of these changes in the concentration of the solution during the growth of the plant was to imitate certain of the conditions actually existing in the soil solution during the growth of the plant, as noted in the investigations of Burd (*6*), Stewart (*42*), and the author (*17*). These experiments showed very clearly that the soil solution diminished in concentration after the plant had grown 8 to 10 weeks. Nitrates at this period almost disappeared. Nevertheless, even with this exhaustion of the soil solution after 8 to 10 weeks, the plants completed their cycle growth, and in most of the soils the ripened crop (after 16 weeks) was characterized by a high yield of both straw and grain. It must follow, therefore, that such a change in the concentration and composition of the nutrient solution at the particular time in question is in no way unfavorable to crop production.

The data presented in Table IV may be considered in the light of the foregoing discussion. While there is considerable variability present, the results may reasonably be accepted as indicating the general trend.

The average yield from the four jars in which the solution was changed to one of low concentration after 6 weeks was possibly inferior to that of the other cultures; but the jars in which the concentration was reduced after 9 weeks gave an equal yield of grain and nearly equal yield of straw, as compared with the cultures in which the highest concentration was maintained for 12 weeks. The initial concentration of 1.95 atmospheres may have had an inhibitive effect, even though later the solution

was reduced to a more favorable concentration. An initial concentration of 3 atmospheres was decidedly injurious.

TABLE IV.—*Weight, composition, and total absorption per plant*

SAND CULTURES, SERIES 3

Part of plant analyzed.	Concentration of solutions and time of application.	Dry weight per plant.[a]	Composition (on water-free basis). N.	P.	K.	Ca.	Mg.
	Atmospheres.	*Gms.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*
Stems and leaves.	0.95 for 6 weeks: 0.15 for 10 weeks	11.2	1.06	0.27	2.78	1.08	0.38
	.95 for 9 weeks: .15 for 7 weeks	13.9	1.49	.36	3.86	.96	.28
	.95 for 12 weeks: .15 for 4 weeks	13.4	2.48	.52	4.95	1.07	.33
	1.95 for 6 weeks; .95 to .15 for 10 weeks	10.5	1.38	.42	4.04	1.20	.29
	3.00 for 6 weeks; .95 to .15 for 10 weeks	7.8	1.40	.44	3.05	1.19	.33
Heads.	.95 for 6 weeks; .15 for 10 weeks	7.8	2.77	.67	.89	.20	.23
	.95 for 9 weeks; .15 for 7 weeks	10.6	2.75	.64	.86	.18	.22
	.95 for 12 weeks; .15 for 4 weeks	9.9	2.93	.70	1.08	.23	.22
	1.95 for 6 weeks; .95 to 15 for 10 weeks	9.1	2.62	.69	.73	.22	.22
	3.00 for 6 weeks; .95 to .15 for 10 weeks	5.9	2.81	.70	.96	.22	.23
Roots.	.95 for 6 weeks: .15 for 10 weeks	3.9	.84	.17	.47	.27	.13
	.95 for 9 weeks; .15 for 7 weeks	7.1	.61	.24	.45	.47	.08
	.95 for 12 weeks; .15 for 4 weeks	4.0	.97	.12	.77	1.76	.15
	1.95 for 6 weeks: .95 to .15 for 10 weeks	3.5	.72	.42	.58	.58	.67
	3.00 for 6 weeks: .95 to .15 for 10 weeks	2.8	.55	.44	.53	.78	.77

Part of plant analyzed.	Concentration of solutions and time of application.	Dry weight per plant.[a]	Total quantities absorbed. N.	P.	K.	Ca.	Mg.
	Atmospheres.	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*
Stems and leaves.	0.95 for 6 weeks: 0.15 for 10 weeks	11.2	0.119	0.031	0.311	0.121	0.043
	.95 for 9 weeks; .15 for 7 weeks	13.9	.208	.050	.538	.134	.039
	.95 for 12 weeks: .15 for 4 weeks	13.4	.332	.070	.662	.143	.044
	1.95 for 6 weeks; .95 to .15 for 10 weeks	10.5	.145	.045	.424	.126	.031
	3.00 for 6 weeks; .95 to .15 for 10 weeks	7.8	.109	.034	.237	.093	.026
Heads.	.95 for 6 weeks; .15 for 10 weeks	7.8	.216	.052	.070	.016	.018
	.95 for 9 weeks; .15 for 7 weeks	10.6	.290	.068	.091	.019	.023
	.95 for 12 weeks: .15 for 4 weeks	9.9	.290	.069	.107	.023	.022
	1.95 for 6 weeks; .95 to .15 for 10 weeks	9.1	.239	.063	.067	.020	.020
	3.00 for 6 weeks; .95 to .15 for 10 weeks	5.9	.165	.041	.056	.013	.014
Roots.	.95 for 6 weeks: .15 for 10 weeks	3.9	.033	.007	.018	.011	.005
	.95 for 9 weeks; .15 for 7 weeks	7.1	.044	.017	.032	.034	.006
	.95 for 12 weeks; .15 for 4 weeks	4.0	.039	.047	.031	.070	.006
	1.95 for 6 weeks; .95 to .15 for 10 weeks	3.5	.025	.015	.020	.020	.024
	3.00 for 6 weeks; .95 to .15 for 10 weeks	2.8	.015	.012	.015	.022	.021

[a] Averages of 16 plants, except in two highest concentrations in which averages are calculated for eight plants. Mean deviation approximately ± 2 gm.

The inference from these results is that an optimum concentration and supply of nutrients must be furnished to the plant for perhaps 8 or 10 weeks. Burd's (7) investigations have already shown that very little absorption from the soil takes place during the first 3 weeks of growth, so it must follow that the most critical period extends over only 6 or 7 weeks. If the nutrient medium is favorable during this period, a very low concentration or small supply may suffice for the remainder of the season, although, as will be proved later, active absorption may continue much longer if suitable solutions are provided. Furthermore, we gain the impression from this experiment that concentrations above 2 atmospheres are too great for the barley plant and that the initial stunting is not entirely overcome by a subsequent change to a more favorable

condition. Other pot experiments with soils uphold this view. When a mixed fertilizer was added to the soil so as to produce, by the freezing-point method, an osmotic pressure similar to that just mentioned, equally striking inhibitive effects were noted.

The data for the total quantities and the percentages in the composition are very definite and confirm the conclusions drawn from series 2. Again we find K and N stored in the tops, while the principal accumulation of Ca and P is in the roots. The heads are only slightly affected in their percentages. Evidently not only concentration but the period during which the concentration is maintained markedly influence the percentage of inorganic elements and the total quantity absorbed per plant. These factors of concentration and period of maintenance of concentration in the soil solution doubtless govern the variations of the plant in its content of inorganic elements under any particular climatic conditions.

WATER CULTURES, SERIES 1

Although the method of sand culture devised by McCall offers very great advantages in control, it is not easily possible to determine the exact composition of the solution at any given time. In order to make an intensive study of the influence of the solution on the plant, and of the plant on the solution, it became necessary to employ the method of solution culture. The technic adopted differed from that in general use in that fewer plants and larger volumes of solution were employed. Observations were made at all stages of growth to maturity. The first experiments were carried out in the greenhouse during the winter months, and the later series were placed out of doors in good light during the spring and summer months.

The first series of experiments was planned to furnish preliminary information with regard to the optimum concentration and the relation of concentration to absorption and transpiration. One-liter bottles were used, with 3 plants in each bottle. Solutions were changed every 3 days after the plants had started to make appreciable growth. After 54 days the plants were cut and the dry weight determined. Four concentrations of solution were tested, and for each concentration there were 8 jars, or 24 plants. The composition of the solution was similar to that given by Shive (*39*) for his best cultures. Table V summarizes the most important results obtained from this experiment.

The data indicate that for these conditions a concentration of 0.10 atmosphere is sub-optimum and one of 2 atmospheres super-optimum. Concentrations of 0.32 and 0.85 atmospheres were equally efficient if we consider the mean deviation in the yields of individual plants. The greatest total transpiration occurred in solution 2. Transpiration per unit of dry weight was decidedly greater in lower concentrations.

TABLE V.—*Effect of concentration on growth and transpiration*

WATER CULTURES, SERIES I

Approximate concentration of solution.	Osmotic pressure.	Number of plants.	Total dry weight of tops.	Average dry weight of tops.	Mean deviation.	Total dry weight of roots.	Transpiration per gram dry weight of tops.
P. p. m.	*Atmos.*		*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
200	0.10	24	12.90	0.54	±0.07	3.4	906
800	.32	24	22.95	.95	±.15	4.0	712
2,500	.85	24	21.65	.90	±.10	4.8	593
6,000	2.07	24	15.50	.65	±.09	3.5	624

A series of sand cultures was carried out to parallel the water cultures; but since there was some indication that the paraffine seal had exercised an inhibitive effect on the growth of the plants, these data are omitted. The evidence obtained, however, led to the conclusion that the transpiration per unit of dry weight was greater in the sand cultures than in the water cultures. This is in accord with the findings of Bouyoucos (*2*).

The absorption studies were made by means of conductivity measurements. In each case comparisons were made under identical conditions between solutions before and after contact with the plant. The general trend of absorption is expressed in a graph. The absorption has been calculated in terms of parts per million of total electrolytes absorbed, based on concentration of the original solution.

The total absorption is evidently greater in the solutions of higher concentration, but in the solution of highest concentration there were two periods when an increase was noted in the concentration of the solution after contact with the plant. It may be inferred that the plant had absorbed in the preceding period such an excess of one or more ions as to cause a temporary reversal of the absorption processes, with a return of ions to the solution. These fluctuations are undoubtedly related in some way to the general light and temperature conditions affecting growth. In later experiments carried on out of doors during the spring and summer the absorption followed a more uniform course. In the greenhouse experiment, light conditions were not favorable to a high yield, and considerable fluctuations in temperature occurred.

In almost all experiments designed to show the relation of the concentration of the solution to absorption and transpiration, the seedlings have been grown from the beginning in the solutions which it was desired to investigate. Any nutritive deficiencies in the solution would thus be reflected in the development of the plant, and the fundamental relations would be obscured. It would seem that the problem might be simplified by growing the plant in a favorable nutrient solution until it had reached a stage of active absorption and then transferring it for a

comparatively short period to any desired solution. A large number of plants may be developed to a uniform stage, and we may then compare different solutions from which absorption is taking place with plants of equal leaf and root development. In brief, the plant is regarded merely as a controlled absorbing system to be investigated.

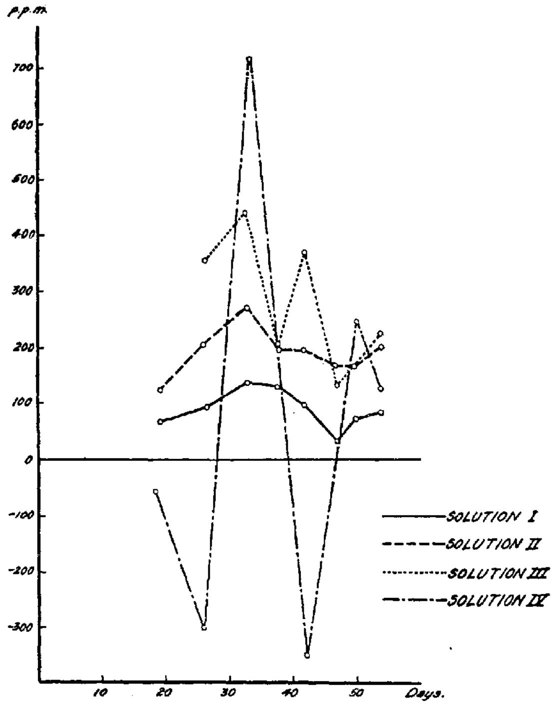

FIG. 1.—Water cultures, series 1. Graph showing net absorption in parts per million from solutions of four concentrations:

Solution I with concentration of 0.10 atmospheres.
Solution II with concentration of 0.32 atmospheres.
Solution III with concentration of 0.85 atmospheres.
Solution IV with concentration of 2.07 atmospheres.

Such a procedure was accordingly carried out in the next experiment. Fifty-six uniform seedlings (2 in each 1-liter bottle) were grown for several weeks in a nutrient solution of 0.85 atmospheres concentration. At the end of this period the bottles were divided into four groups. After the roots were rinsed with distilled water the plants were trans-

ferred to solutions of the four different concentrations previously mentioned. The absorption and transpiration were then determined for a period of two days, after which the plants were cut and the dry weight determined.

TABLE VI.—*Transpiration and absorption by uniform plants*

WATER CULTURES, SERIES I

Approximate concentration of solution.	Osmotic pressure.	Average dry weight of tops.	Transpiration per gram dry weight of tops.		Average absorption of electrolytes from each jar.
			First day.	Second day.	
P. p. m.	*Atmos.*	*Grams.*	*Grams.*	*Grams.*	*P. p. m.*
200	0. 10	0. 43	50	94	−25
800	. 32	. 46	46	91	72
2, 500	. 85	. 50	34	64	288
6, 000	2. 07	. 50	33	48	402

These results are interpreted to mean that the concentration of the solution has a marked effect on absorption and transpiration. Almost double the quantity of water per gram of dry weight is transpired by the plants in the solution of lowest concentration as compared with the quantity transpired by those in the highest concentration. In the solution of lowest concentration there was possibly a slight excretion of electrolytes from the plant. In the other solutions absorption took place in the order of increasing concentrations.

It has sometimes been assumed that transpiration may be regarded as proportional to the dry weight of the plant and that the effect of various solutions may be reflected in the transpiration. Livingston (*24*) and Whitney and Cameron (55) have tended toward this view; on the other hand Bouyoucos (*2*) has found that the concentration of the nutrient solution has a decided influence on transpiration, the higher concentrations diminishing water loss, either because of the difficulty experienced by the plant in absorbing water from a solution of higher osmotic pressure or because the increased osmotic pressure of the cell sap decreased the vapor tension and so reduced transpiration. Our experiments uphold the view that solutions of increased concentration have the effect of reducing transpiration. Since plants of uniform development and approximately equal leaf surface display widely different transpiration rates with solutions of different concentrations, it does not appear that transpiration is necessarily an accurate criterion of growth. There is, in fact, a preponderance of evidence to show that transpiration per unit of dry weight increases with decreasing concentration. Kiesselbach (*21*) and Khankhoje (*20*) reached this conclusion as a result of sand-culture studies, while Preul (*35*) and Kiesselbach found that the water requirement per unit of dry weight is less on a poor soil. Widtsoe (*54*) says that fallowing and fertilization decreased the water requirement.

These observations on soils are in harmony with the work of Stewart (42) and the author (17), who found that the concentration of the soil solution may be increased by fallowing and decreased by cropping.

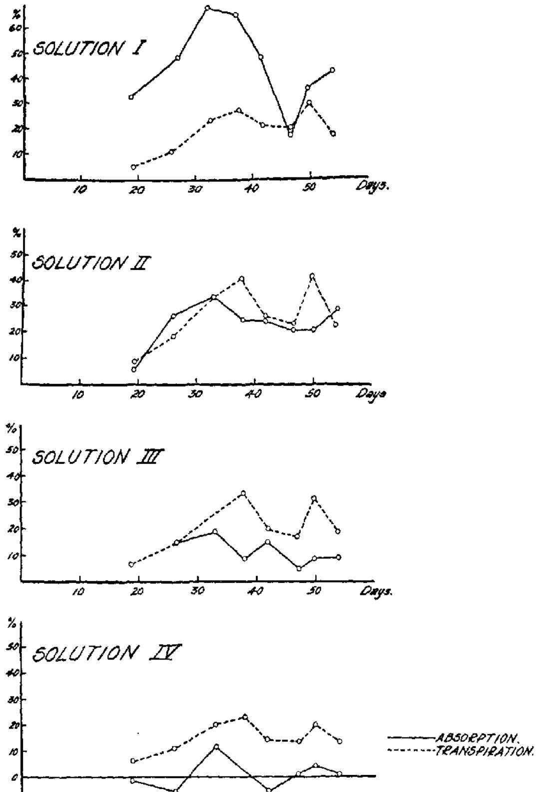

FIG. 2.—Water cultures, series 1. Graphs showing comparison between percentage of total nutrient absorbed and percentage of total water transpired with solutions of four concentrations.

The relation between absorption and transpiration are shown in figure 2. The data have been calculated in terms of percentage of total water transpired and percentage of total nutrients absorbed. Very different

results are given by the different concentrations. In the lowest concentration the percentage of water transpired is much less than the percentage of electrolytes absorbed. In the highest concentration this relation is reversed, and in the intermediate concentration of 0.32 atmospheres the two percentages are essentially the same. It is quite clear that absorption may proceed independently of transpiration, and that the plant may absorb and transpire at such rates as either to increase or decrease the concentration of the nutrient solution. This is in general agreement with the views of Pantanelli (*32*).

WATER CULTURES, SERIES 2

This series was planned for the purpose of making certain observations on absorption and growth when plants were grown to maturity. Two-liter bottles were used, and only one plant was placed in each bottle. The experiment was started on February 11. During the first 10 weeks, up to the time of heading out, a solution of 0.78 atmospheres concentration was used, the solution being changed about once each week. The composition of the solution was similar to that used in sand cultures, series 2. The plants were grown out of doors, and at this season the growth rate was fairly slow. On April 27 the plants were divided into 3 groups of 10 plants each and the solution changed to 3 different concentrations, 0.10, 0.30, and 0.80 atmospheres, respectively. Thereafter the solutions were not changed. The object of this procedure was to gain some insight into the growth and absorption of the plant when the concentration of the solution was diminished during the latter part of the growth cycle, a condition somewhat analogous to that in the soil.

The plants completed the growth cycle and produced matured heads. There were from 5 to 10 tillers on each plant. Most of the heads were out by May 17, and by June 24 the hard dough stage was reached. The plants were cut July 16, about five months after planting. A marked difference in appearance was noted in the three groups. Although water was, of course, not a limiting factor in the concentration of 0.10 atmospheres, the plants turned yellow sooner and more completely than in the higher concentrations. In the highest concentration considerable green color persisted to the end of the experiment, but the heads from the lowest concentration were slightly superior. In the highest concentration the ripening was slow and there was some indication of shrinkage of the grain before the period of desiccation. The total yields as shown below are greater in the higher concentrations, although there is no significant difference between the concentrations of 0.10 and 0.30 or 0.80 atmospheres, for the yield of heads and even the difference in the yields of stems and leaves are not necessarily significant.

AIR-DRY WEIGHT PER PLANT.[a]

Concentration of solution.	Heads.	Stems and leaves.	Roots.
Atmospheres.	*Grams.*	*Grams.*	*Grams*
0. 10	10. 2	10. 6	0. 44
. 30	10. 7	12. 7	. 30
. 80	12. 0	15. 4	. 77

[a] Based on 10 plants.

The conclusion may be drawn from the foregoing observations that the greater concentration or supply of one or more ions present during the later stages prolongs the period of vegetative growth and possibly interferes with the processes of ripening, without producing any large increase in yield.

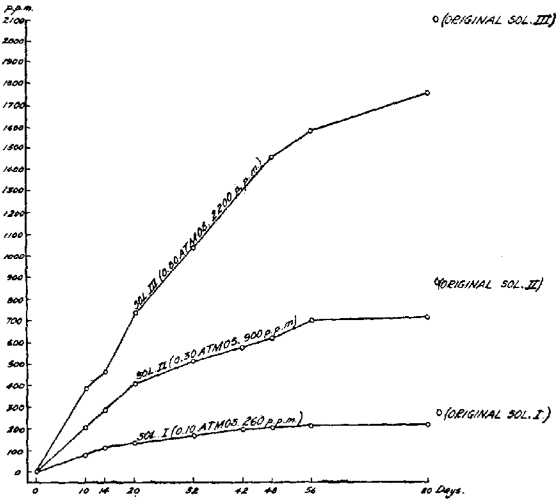

FIG. 3.—Water cultures, series 2. Graph showing absorption of nutrients from solutions of three concentrations during latter part of growth cycle. Solutions not changed during the final 80 days.

The absorption was followed each week by means of conductivity measurements, by removing portions of solutions from the culture bottles after adding water to restore the original volume. The solution was thoroughly mixed by passing a current of air through it. After the conductivity was determined the samples were returned to the original bottles. The course of absorption is graphically indicated in figure 3. The data are calculated to percentages of total electrolytes absorbed

on the basis of the original solution. At the end of the experiment composite samples were made of each solution, and these were analyzed for the important elements present. The results are shown in Table VII.

TABLE VII.—*Analyses of nutrient solutions of different concentrations after growth of plant*

WATER CULTURES, SERIES 2

Approximate concentration of solution.	Osmotic pressure.	Composition of solution after growth of plants.						Percentage of absorption by plant.					
		NO_3.	PO_4.	K.	Ca.	Mg.	SO_4.	NO_3.	PO_4.	K.	Ca.	Mg.	SO_4.
P. p. m.	*Atmos.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*						
260	0.10	0	3.1	4.3	11.5	2.7	7.4	100	76	87	66	78	85
900	.30	0	5.4	12.2	35.0	12.0	38.3	100	88	89	70	69	75
2,200	.80	12.5	1.8	43.7	87.0	35.0	105.0	99	98	85	70	64	73
[a] 1,300	.45	0	1.4	6.0	63.0	13.0	42.0	100	99	96	62	60	68

[a] Solutions not changed for 16 weeks.

Absorption continued until a large percentage of the total ions present were absorbed. In two cases the NO_3 ion was completely removed. The Ca, Mg, and SO_4 were absorbed in lesser percentage than the NO_3, PO_4, and K. The percentages of absorption for the given ions were not dissimilar in the three concentrations; therefore, under these conditions, the total absorption was approximately proportional to the concentration of ions present in the original solution. In the supplementary cultures in which the solutions were not changed between the ages of 6 weeks and maturity, practically all of the NO_3, PO_4, and K have been removed from the solution. It is interesting to note, however, that 100 per cent removal is effected only in the NO_3 ion. This fact may perhaps be explained by the nature of the metabolic processes in the plant. The NO_3 ion undergoes complete chemical transformation, and at certain stages may disappear entirely from the sap, while the other ions are always present. Thus the equilibrium conditions would differ in the two cases.

In the third series of water cultures the procedure was varied by changing the nutrient solution regularly each week throughout the whole growth of the plant, for 15 weeks. At each change of solution conductivity measurements were made, and the average absorption of electrolytes for the week was computed. The plants were grown two in each jar of approximately 1,000-cc. capacity. After 10 weeks part of the jars were changed to a concentration of 0.10 atmospheres, while the other were continued with concentrations of 0.90 atmospheres. In each case both neutral (P_H 6.5 to 6.8) and acid (P_H 5.1 to 5.5) solutions were compared under otherwise similar conditions. The composition of the solutions is given in Table VIII.

TABLE VIII.—*Composition of nutrient solutions*

WATER CULTURES, SERIES 3

Osmotic pressure.	P_H.	NO_3.	PO_4.	K.	Ca.	Mg.	SO_4.
Atmos.		*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*	*P. p. m.*
0.10	5.5	88	14.4	19.8	23.7	8.9	27.5
.10	6.5	80	10.6	20.3	22.9	9.4	31.6
.90	5.1	1,100	180.0	248.0	296.0	90.0	344.0
.90	6.8	1,000	132.0	252.0	286.0	102.0	395.0

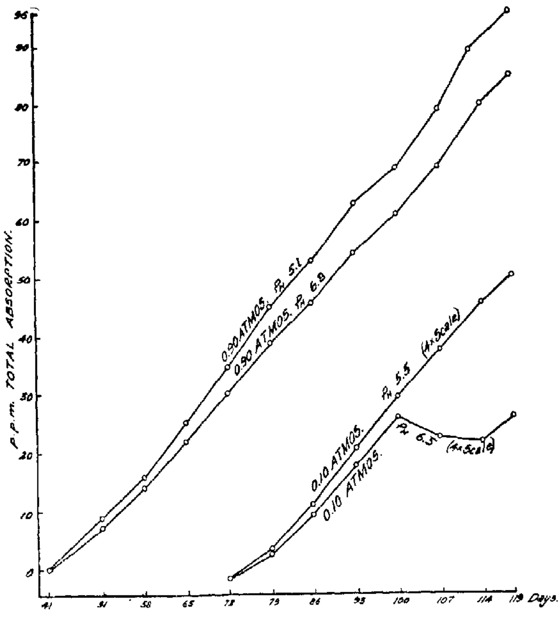

FIG. 4.—Water cultures, series 3. Graph showing absorption of nutrients from solutions of two concentrations and two reactions. Solutions changed weekly.

In figure 4 the course of absorption is shown graphically, and comparisons may be made with figure 3. The absorption is plotted for convenience as parts per million of total electrolytes absorbed, the calculations being based on the conductivities of the solutions. These graphs demonstrate clearly that in solutions of 0.10 atmospheres concentration (P_H 5.5), of 0.90 atmospheres (P_H 6.8), and of 0.90 atmospheres (P_H 5.1) absorption continues in a fairly uniform way for the entire time. The

solution of 0.10 atmospheres concentration (P_H 6.5), however, gives a different type of curve. During the fourteenth to sixteenth weeks, electrolytes instead of being absorbed were returned to the nutrient solution. During the final week absorption was again resumed.

These measurements are particularly interesting, since Burd (7) has observed an analogous phenomenon in the absorption of barley plants grown in soils. In this investigation plants were cut and analyzed at various stages of growth in such a way that the total content of the important elements could be calculated on the basis of an average plant. At a certain period in the growth cycle, which coincided approximately with the period of lowest concentration in the soil solution, there was a marked loss of K and N from the tops of the plants together with a small loss of Ca, Mg, and PO_4. After several weeks, absorption, or at least a return of elements to the tops of the plants, again took place. Although in a soil experiment it is not possible to recover roots quantitatively, it is thought probable that a considerable portion of the elements lost from the tops returned to the soil. Certainly in the solution-culture experiment, electrolyte concentration increased in the solution mentioned. This did not occur, however, in those solutions in which the higher concentration was maintained nor in the solution of low concentration with an acid reaction. The latter fact may receive a possible explanation in some experiments dealing with the effect of hydrogen-ion concentration, to be discussed later in the article.

The plants grown in this series, as in series 2, remained green in the higher concentration. The heads ripened, but a good deal of the grain had a shrunken appearance. The yields in terms of air-dry weight are as follows:

Osmotic pressure.	P_H.	Average weight per plant.[a]	
		Straw.	Heads.
Atmos.		*Grams.*	*Grams.*
0.10	5.5	13.0	7.7
.10	6.5	12.8	7.4
.90	5.1	19.3	8.2
.90	6.8	17.5	7.0

[a] Based on 10 plants.

The dry weight of the straw is somewhat greater where a higher concentration of solution has been maintained, but the yield of heads is not significantly different.

WATER CULTURES, SERIES 4

This series had for its object the comparison of yields in solutions of various concentrations and the determination of the absorption of each ion from the different solutions during a given period of time. One-liter bottles were employed with 2 plants in each bottle. Solutions were

changed every two days in the lower concentrations and every three days in the others. Ten bottles with 20 plants were used for each solution. Four concentrations were tested 0.07, 0.58, 0.90, and 1.70 atmospheres. In each concentration, solutions of both acid and neutral reaction were subjected to experiment. The composition of the solutions was such that in each concentration the acid and neutral solutions had practically identical freezing-point depressions and as nearly as possible the same ionic ratios. The exact composition of the solutions is given in Table VIII. The plants were grown out of doors in a uniform light from June 26 to August 22. The bottles were so arranged and changed in position that the light and temperature conditions were essentially the same for all cultures.

When the plants had grown for 6 weeks, the absorption study was made for a period of 72 hours. The original solutions were analyzed for Ca, Mg, PO_4, NO_3, K, and SO_4; and the same solutions after contact with the plant and after they had been made up to original volume were again analyzed. The differences between the two analyses represent the change in concentration due to 72 hours' absorption by the plant, expressed as parts per million of the various ions. The total quantities removed are obtained by multiplying the parts per million change by the volume of the solution.

The data incorporated in the above table furnish a basis for a number of interesting suggestions concerning absorption. In the first place it is noted that in the lowest concentration the percentage of absorption for all elements is much greater than in the two highest concentrations. This is in accord with the results from the first series of water cultures. The total quantities absorbed per plant are much greater in the concentration of 0.90 atmosphere as compared with 0.07 atmosphere, but in the highest concentration there is no corresponding increase and in a number of instances there is a decrease. If a large number of solutions were employed with small increments in concentration, we may infer that the total quantities absorbed would increase up to a certain total concentration and then would remain constant or decrease. Since the percentage of absorption, however, might be different there would not be necessarily a direct proportionality between the concentration of each ion and the quantity absorbed. Some data are cited by Pouget and Chouchak (*34*) in support of the assertion that NO_3 absorbed by wheat seedlings is proportional to the concentration up to a certain point. This could not be finally decided except under conditions which permitted absorption studies with controlled conditions of concentration over various time periods.

TABLE IX.—*Absorption from solutions of various concentrations and reactions in a 72-hour period by plants 7 weeks old*

WATER CULTURES, SERIES 4

COMPOSITION (IN PARTS PER MILLION OF ORIGINAL SOLUTIONS)

Osmotic pressure.	P_H.	NO_3.	PO_4.	K.	Ca.	Mg.	SO_4.
Atmos.							
0. 07	5. 5	88	14. 4	19. 8	23. 7	8. 9	27. 5
. 07	6. 5	80	10. 6	20. 3	22. 9	9. 4	31. 6
. 88	5. 1	1, 100	180. 0	248. 0	296. 0	90. 0	344. 0
. 89	6. 8	1, 000	132. 0	252. 0	286. 0	102. 0	395. 0
1. 72	4. 9	2, 200	354. 0	500. 0	560. 0	183. 0	697. 0
1. 70	6. 1	2, 000	222. 0	501. 0	536. 0	202. 0	770. 0
ABSORPTION (IN PARTS PER MILLION OF SOLUTION)							
0. 07	5. 5	88	12. 9	19. 0	10. 2	4. 2	9. 8
. 07	6. 5	80	9. 4	19. 4	7. 4	3. 4	11. 7
. 88	5. 1	421	71. 0	74. 0	52. 0	8. 0	34. 0
. 89	6. 8	244	35. 0	77. 0	22. 0	22. 0	26. 0
1. 72	4. 9	322	124. 0	38. 0	48. 0	17. 0	39. 0
1. 70	6. 1	345	78. 0	61. 0	48. 0	21. 0	45. 0
NUMBER OF GRAMS ABSORBED PER PLANT)							
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
0. 07	5. 5	0. 044	0. 006	0. 010	0. 005	0. 002	0. 005
. 07	6. 5	. 040	. 005	. 010	. 004	. 002	. 006
. 88	5. 1	. 210	. 035	. 037	. 026	. 004	. 017
. 89	6. 8	. 122	. 017	. 038	. 011	. 011	. 013
1. 72	4. 9	. 161	. 062	. 019	. 024	. 008	. 019
1. 70	6. 1	. 172	. 039	. 030	. 024	. 010	. 022
PERCENTAGE OF ABSORPTION							
0. 07	5. 5	100. 0	89. 6	96. 0	43. 0	47. 2	35. 7
. 07	6. 5	100. 0	88. 6	95. 6	32. 3	36. 2	37. 0
. 88	5. 1	38. 2	39. 5	29. 8	17. 6	8. 9	9. 9
. 89	6. 8	24. 4	26. 5	30. 6	7. 7	21. 6	6. 6
1. 72	4. 9	14. 7	35. 0	7. 6	8. 5	9. 3	5. 6
1. 70	6. 1	17. 2	35. 1	12. 2	9. 0	10. 4	5. 9

In the solutions of 0.07 atmospheres concentration, it is significant that all the NO_3 ions and nearly all the K and PO_4 ions were absorbed within 72 hours. It is not possible to say from these data just how the absorption was distributed over the period of time in question, but it is logical to suppose that the total quantities absorbed per hour decreased until finally in the NO_3 ion every trace had disappeared from the solution.

The air-dry yields are given in Table X. Plants from each jar were weighed separately in order to gain some idea of the mean deviation and thus provide a basis for judging the significance of the results.

TABLE X.—*Yields of tops and roots*

WATER CULTURES, SERIES 4

[Plants grown for eight weeks]

Osmotic pressure.	P_H.	Average air-dry weight of tops per plant.	Mean deviation for 18 plants.	Average air-dry weight of roots per plant.	Mean deviation for 14 plants.
Atmos.		*Grams.*	*Grams.*	*Grams.*	*Grams.*
0.07	5.5	2.9	±0.15	0.56	±0.05
.07	6.5	2.9	± .15	.62	± .03
.58	5.1	7.4	± .50	1.19	± .21
.56	6.8	7.0	± .60	1.24	± .15
.88	5.1	8.1	±1.00	1.39	± .19
.89	6.8	5.8	±1.00	.95	± .13
1.72	4.9	3.8	± .60	1.09	± .15
1.70	6.1	4.5	± .50	.92	± .17

The yields from concentrations of 0.07 atmospheres and 1.70 atmospheres are decidedly inferior to those from concentrations of 0.58 atmospheres and 0.90 atmospheres. Between the two latter there is no significant difference. The yields of plants from the acid solution are at least equal and possibly superior to those from the neutral solution. Certainly there is no evidence of inhibition in the acid solutions, except with the highest concentration. This is a super-optimum concentration for both acid and neutral solutions; but in the acid solution of this highest concentration the roots were distinctly injured, while those in the corresponding neutral solution had a more normal appearance. In the other solutions of similar hydrogen-ion concentration the roots were quite uninjured. In other words, the injury referred to was the resultant effect of the hydrogen-ion concentration and super-optimum total concentration, or more specifically, perhaps, due to the high concentration of PO_4 in the acid solution. A much larger quantity of PO_4 was absorbed in the latter case.

It should be emphasized in connection with the relative yields that the most dilute solution was exhausted of its NO_3 in less than 72 hours. The question then arises, whether the diminution in yield might not be due to a deficiency in total quantity of one or more ions rather than to sub-optimum concentration.

This suggestion led to a further water-culture experiment, series 5. Twenty plants were grown in bottles of 2,200-cc. capacity with only 1 plant in each bottle. Solutions were changed, after the first few weeks, about five times each week. In this way, as analysis showed, the solutions were maintained practically constant. The composition of the solutions was similar to that described before, two concentrations being used of 0.07 atmospheres and 0.58 atmospheres. After seven weeks the plants were cut and weighed in the air-dry state. The concentration of 0.07 atmospheres gave a yield of 0.60±0.08 gm. of tops and 0.20 gm. of

roots per plant, and the 0.58 atmospheres concentration a yield of 0.66 ± 0.08 gm. of tops and 0.24 gm. of roots. Between these figures there is no significant difference, although in water cultures, series 1 and series 4, similar solutions gave distinctly different yields. To verify these results finally it will be necessary to repeat the experiment at a more favorable season of the year; but we may reasonably conclude, taking all the experiments into consideration, that with a solution of the general composition described above the optimum concentration for the barley plant—defined as the least concentration producing a yield equal to any higher concentration—is not higher than 0.60 to 0.90 atmospheres and may be less than 0.10 atmospheres. This point is to be considered more critically in the final discussion.

In one of the preceding experiments reference was made to the observation that under certain conditions electrolytes might leave the plant and return to the solution. In order to gain some additional insight into this process, a number of plants which had grown for 6 weeks in favorable nutrient solutions were transferred to various very dilute nutrient solutions after washing the roots thoroughly in distilled water. The results are presented in Table XI, in which comparisons are made between the resistances of original solutions and the same solutions after contact with the plant.

TABLE XI.—*Absorption by plants from dilute solutions*

Concentration of nutrient solution.	Resistance of original solutions.	Resistance of solutions after contact with plants for—							
		4 days.	7 days.	14 days.[a]	19 days.	28 days.	35 days.	42 days.	49 days.
P. p. m.	*Ohms.*	*Ohms.*	*Ohms.*	*Ohms.*	*Ohms.*	*Ohms.*	*Ohms.*	*Ohms.*	*Ohms.*
25	3, 380	1, 190	1, 290	5, 940	16, 300	25, 200	5, 300	5, 630	5, 390
75	1, 150	850	1, 090	1, 620	5, 580	15, 200	16, 500	3, 420	9, 230
150	630	530	600	1, 050	1, 630	6, 540	8, 290	10, 050	10, 400
300	340	400	475	610	860	3, 180	5, 800	4, 590	6, 130
500	210	275	390	350	470	1, 880	4, 600	7, 170	6, 130

[a] Solutions changed.

In the two most dilute solutions the electrolyte concentration was increased, and from the three higher concentrations absorption took place. Later absorption occurred from all solutions, so that in several cases the resistance of the solutions became about the same as that of the distilled water used. Subsequently there was a further excretion of electrolytes from the plant. True and Bartlett (49, 50, 51) have described phenomena similar to these, working with partial nutrient solutions in very great dilution.

True (*48*) has also pointed out that distilled water may be injurious because of the elements leached out from the plant. In order to ascertain which elements would leave the plant we have transferred a number of

plants as described above to distilled water and after several days have analyzed the solution. The composition was found to be as follows:

	P. p. m.		P. p. m.
NO_3	None.	Ca	19.0
PO_4	5.7	SO_4	None.
K	1.2	Mg	1.7

Ca and PO_4 were thus the principal elements leached out. It will be recalled that in sand cultures of series 2 and 3 considerable accumulation of Ca and PO_4 occurred in the roots.

In order to compare absorption at different periods of the growth cycle, analyses of solutions were made after the plants had absorbed for a period of a week from solutions of 0.90 atmospheres concentration with reactions of P_H 5.1 and 6.8. The periods chosen were 4 to 5 weeks, 6 to 7 weeks, and 11 to 12 weeks. In Table XII are shown the total quantities per plant and percentages of the various elements absorbed.

TABLE XII.—*Absorption of elements at different stages of growth* [a]

[Absorption period seven days]

Period of growth.	Osmotic pressure.	P_H.	NO_3.	PO_4.	K.	Ca.	Mg.	SO_4.
PARTS PER MILLION OF SOLUTION ABSORBED								
	Atmos.							
4 to 5 weeks	0.88	5.1	384	60	90	48	8	42
Do	.89	6.8	157	43	65	28	9	73
6 to 7 weeks [b]	.88	5.1	536	108	126	92	20	71
Do	.89	6.8	416	61	125	61	16	65
11 to 12 weeks	.88	5.1	545	146	107	84	17	72
Do	.89	6.8	325	93	112	74	23	81
NUMBER OF GRAMS ABSORBED PER PLANT								
4 to 5 weeks	0.88	5.1	.192	0.030	0.045	0.024	0.004	0.021
Do	.89	6.8	.078	.021	.032	.014	.004	.011
6 to 7 weeks	.88	5.1	.268	.054	.063	.046	.010	.035
Do	.89	6.8	.208	.030	.062	.030	.008	.032
11 to 12 weeks	.88	5.1	.272	.073	.053	.042	.008	.036
Do	.89	6.8	.162	.046	.066	.037	.011	.040
PERCENTAGE OF TOTAL QUANTITY ABSORBED								
4 to 5 weeks	0.88	5.1	34.8	34.6	34.7	15.9	9.0	12.2
Do	.89	6.8	15.7	37.7	23.0	9.7	9.3	6.0
6 to 7 weeks	.88	5.1	48.6	61.8	48.0	30.5	22.5	20.6
Do	.89	6.8	41.6	53.5	44.2	21.2	16.5	16.0
11 to 12 weeks	.88	5.1	49.4	81.0	43.1	28.4	18.8	20.9
Do	.89	6.8	32.5	70.5	44.5	25.9	22.6	20.5

[a] Studies made on composite solutions, each representing 20 plants with 2 plants per liter of solution.
[b] Computed from 9-day absorption period.

It will be noted that the total quantities and percentages were considerably greater in the two later periods as compared with the first period. Absorption in the eleventh to twelfth weeks was not greatly different from that in the sixth to seventh weeks, except that in the latter period the absorption of PO_4 was decidedly increased. In each period the absolute quantity of PO_4 absorbed from the acid solution exceeded that from the

neutral solution. This is also true of several other elements, particularly NO_3, although the concentration of NO_3 was approximately the same in the original acid and neutral solutions. The concentration of PO_4 was, of course, greater in the original acid solution.

THE EFFECT OF REACTION ON GROWTH AND ABSORPTION

As was stated earlier in this article, all the nutrient solutions were controlled with respect to hydrogen-ion concentration. This subject has received some previous study in this laboratory. In an earlier investigation (*16*), it was shown that barley seedlings were not injured nor inhibited by a hydrogen-ion concentration of P_H 5. More recent work has confirmed these views for barley plants at all stages. Furthermore, certain reports from the field regarding peat soils have indicated that acidity of an intensity represented by P_H 4.8 or 5 is not injurious to a large number of common agricultural plants.

In some of these investigations the interesting fact was discovered that in none of the nutrient solutions examined was there any tendency for the plant to produce an excessive concentration of hydrogen or hydroxyl ion, but that the opposite was true. Both alkaline and acid solutions were brought approximately to the neutral point as a result of absorption by the plant. In the water cultures of series 3, hydrogen-ion concentrations were determined by colorimetric methods at each weekly change of the nutrient solution, as follows:

TABLE XIII.—*Hydrogen-ion concentration of nutrient solutions after absorption by plant for one week*

WATER CULTURES, SERIES 3

Osmotic pressure of original solution.	P_H value of original solution.	P_H value after absorption for—								
		58 days.	65 days.	72 days.	79 days.	86 days.	93 days.	100 days.	107 days.	114 days.
Atmos.										
0.10	5.5	......	......	......	7.2	......	6.3	6.5	6.5	6.8
.10	6.5	......	......	......	7.2	......	6.5	6.5	6.5	6.8
.90	5.1	6.8	7.0	7.2	7.2	7.2	7.2	6.8	7.0	6.8
.90	6.8	6.8	7.0	7.2	7.2	7.4	7.0	6.8	7.0	6.8

At the end of the period of contact with the plant all solutions gave an almost neutral reaction. Control experiments showed that no appreciable change of reaction was due to the glass in contact with the solutions. By referring to Tables IX and XII one may compare the changes of hydrogen-ion concentration with the removal of the various ions from solution. In general it may be said that absorption is so altered in the acid solutions that larger percentages of a number of ions are absorbed, as compared with the corresponding neutral solutions. NO_3 and Ca are particularly affected. In the solution of 0.90 atmospheres concentration and P_H 5.4 a considerably higher percentage of PO_4

was absorbed. In all cases the total quantity of PO_4 absorbed was greater with the acid solutions. The increased absorption from acid solutions is also definitely indicated in figure 4. Here the total ionic absorption as determined by conductivity measurements was consistently greater in the solutions of P_H 5.1 as compared with solutions of P_H 6.8, both of practically the same concentration.

Even when solutions of single salts are used the absorption by the plant does not bring about an unfavorable condition of acidity or alkalinity. To determine the nature of such absorption, plants were grown in favorable nutrient solutions until they had reached a stage of active absorption. They were then transferred to solutions of sodium nitrate ($NaNO_3$), potassium chlorid (KCl), potassium sulphate (K_2SO_4), magnesium sulphate ($MgSO_4$), potassium phosphate (K_3PO_4), and ammonium chlorid (NH_4Cl). From the $NaNO_3$ solution a greater percentage of NO_3 than Na was absorbed, but equilibrium was restored by the formation of carbonic acid (HCO_3) ion. This in equilibrium with carbon dioxid (CO_2) gave to the solution an approximately neutral reaction, nor did other solutions tested acquire an excessive concentration of hydrogen or hydroxyl-ion. K and Cl were found to be absorbed in equivalent quantities. The high alkalinity of the potassium phosphate (K_3PO_4) solution was reduced to a condition of slight alkalinity. Further details of these experiments are reported elsewhere (*18*).

In the complete nutrient solution it is impossible to say exactly what ions and undissociated salts are present before and after absorption by the plant. Such a system, with its various hydrolyzable salts, is very complex. Calculations of reacting values for the various elements present indicate that an excess of acid radicles have been absorbed by the plant, in greater degree from the solutions of acid reaction. These have attained a practically neutral reaction after contact with the plant, as noted above. Since the solution must remain balanced with respect to positive and negative ions, some other ions must have been formed in the solution. Where NO_3 is absorbed in large percentage it is probable that CO_3 or HCO_3 become important constitutents of the solutions. A small quantity of silicate radicles is also found, derived from action on the glass. The resultant reaction is due to the particular state of equilibrium existing among all these constituents; and while we may determine the hydrogen-ion concentration with considerable accuracy, the data at present available do not enable us to determine the exact relations between the different components of the system.

THE EFFECT OF THE NUTRIENT SOLUTION ON THE CELL SAP

That the concentration of the nutrient medium is reflected to a certain extent in the cell sap has been shown by McCool and Millar (*30*). In another article by the present author [1] are described determinations

[1] In course of publication in Bot. Gaz.

on the sap expressed from the tops and roots of the plants grown in water cultures, series 4. Measurements were made of hydrogen-ion concentration, depression of the freezing point, and specific conductivity. It was shown that the total osmotic pressure and conductivity increased with increasing concentration of the nutrient solution. Analyses of the sap of barley plants gave evidence of a very high concentration of ions, many times greater than that found in the soil or nutrient solution. The following figures give an idea of the magnitudes concerned:

	PO^4.	K.	Mg.	Ca.	NO^4.	Total N.
Parts per million of sap ...	800 to 2,000	5,400 to 6,100	270 to 340	600 to 1,000	700 to 2,500	600 to 1,400

The hydrogen-ion concentration of the sap pressed from the tops of barley plants displayed a great constancy. The P_H value of 6.1 was practically the same in the sap of plants from sand, water, and soil cultures, even when the osmotic pressures and conductivities differed greatly.

GENERAL DISCUSSION

Having now presented the data obtained in the course of these investigations, it becomes necessary to survey the experiments as a whole, with the intention of considering certain principles of plant nutrition. It will also be desirable to correlate the present results with those of other investigators. No attempt will be made, however, to give any complete bibliography of the general subject. This has already been done by Tottingham (*45*), Shive (*39*), and Pantanelli (*32*), among others. Only such citations will be made as bear directly upon the questions considered in this article.

Before proceeding further in this discussion, we wish to call attention to one very serious deficiency in the fundamental data necessary to any extension of plant nutrition studies. There appear to be no adequate and systematic experiments capable of showing the variability of plants under favorable and unfavorable conditions, yet such a basis of calculation is indispensable to any proper interpretation of yields, when small variations of nutrient solutions are concerned. This factor has been called to the attention of the author by the work of Waynick (*53*), who has shown how very erroneous may be the conclusions derived from soil studies when the statistical method of interpretation is neglected. These criticisms apply also, at least in large measure, to many investigations in plant nutrition. In the interpretation of the data obtained in our investigations there has been no intention of assigning relative values to a large number of solutions. The whole purpose has been to determine the general magnitudes involved and to explain something of the nature of the course of absorption by the plant, with the hope of gaining further knowledge of the principles involved. It

would seem highly desirable that some sort of critical basis be established before attempting more highly specialized experiments dealing with small variations.

It is of course quite obvious that no control of the soil is possible sufficient to elucidate the fundamental points in plant nutrition. Recourse to water and sand cultures is essential, without question. We may, however, regard the soil as the natural habitat of agricultural plants, and when a high yield is obtained we are justified in assuming that the particular conditions that obtain in the soil solution are not unfavorable to the development of the plant. Any definite information, therefore, which may be obtained regarding the soil solution will serve as a guide to at least one set of favorable factors. Very little is known of the soil solution, but the method perfected by Bouyoucos and McCool (*3*) has enabled us to ascertain with fair accuracy the total osmotic values. This method has been applied in soil investigations conducted by this laboratory, determinations being made at frequent intervals throughout the season. The results were quite definite in showing that about 10 weeks after planting the barley crop had diminished very significantly the concentration of the soil solution. Water extracts indicated that by this particular period very little NO_3 remained in the soil solution. Moreoever, high yields of barley and wheat have been obtained on soils whose solutions at no time during the growth cycle had a concentration greater than 0.5 atmospheres. Similar relations have been observed for a number of other plants. We may conclude from these soil investigations that the plant does not necessarily require a concentration of the nutrient medium higher than the one stated above, and that it is not necessary that the concentration or large supply of NO_3 be maintained during the latter part of the growth cycle.

These facts were made the basis of several water- and sand-culture experiments already described. It became evident from these that at least for the barley plant the normal cycle of development did not require that the concentration of the nutrient solution be maintained after nine weeks for the climatic conditions under which the experiment was conducted. A longer continued maintenance of the concentration leads to no important increase in yield but does cause the plant to attain a very much higher percentage of certain elements. Also when the supply of NO_3 and other elements is constantly replenished, the plant may remain green almost indefinitely. In the soil the particular cycle of development of the plant is related to the diminution in the concentration or total supply of elements in the soil solution, and this diminution itself has been brought about to a large extent as a result of absorption by the plant. We may infer, then, that the most important condition for a high yield, in so far as the soil solution is concerned, is an adequate concentration and supply of nutrients during the first half

of the growth cycle. If the concentration or supply is either sub-optimum or super-optimum during this period, no subsequent favorable condition is likely to produce maximum yield. An inhibitive concentration for barley either in water, sand, or soil cultures is not extremely high, possibly less than 2.5 atmospheres. The minimum concentration giving a maximum yield is low, though the magnitude can not be exactly stated at present. It may not be more than that represented by 0.1 atmospheres osmotic pressure.[1]

Some recent work of Davidson and LeClerc (*9*) bears on certain of the above statements. These investigators give evidence that the greatest increase in yield of wheat is obtained when soil fertilization is accomplished during the first stage of growth, a slighter effect is produced during the second stage, and no effect during the third. An increased percentage of N in the grain occurs when fertilization takes place during the second stage. During the third stage no effect is produced. It is possible that the N content of the grain may be influenced by the length of time during which nitrification continues in the soil, and this latter process may in part be governed by climatic conditions. Very marked seasonal fluctuations in NO_3 have been noted by Stewart (*42*) in soils kept always at optimum moisture content and in an excellent state of cultivation.

Finally, in the consideration of the relation of the soil solution to plant growth it should be pointed out that the interpretation of soil experiments in terms of concentration of the soil solution requires recognition of the fact that the growth of the plant is affected by the properties of the solution in actual contact with the absorbing root membranes. The degree to which nutrient elements are maintained at a favorable concentration in this effective solution must depend upon the rate of diffusion and upon the potentiality possessed by the soil for constant renewal of the solution as elements are absorbed by the plant. The question of diffusion has been discussed by Russell (*36*), while Burd (*6*) has shown the necessity of taking into account the renewing power of the soil. It follows that conclusions drawn from determinations on samples of the whole mass of soil do not imply an exact knowledge of conditions in the solution from which the plants are actually absorbing.

The question of the optimum concentration of solution for barley, wheat, and other grains has been discussed in a number of articles with considerable disagreement in the conclusions. It may be well to define the conditions necessary for the determination of the effect of concentration on plant growth. In such a study it is essential that the concentration of the solution be maintained constant at all times. In other words, as absorption takes place the solution must be renewed. Ideally this can be accomplished only by a continuous flow. Such a technic is

[1] Later experiments show that this concentration is somewhat less than optimum when light and temperature conditions are highly favorable.

usually impracticable, so it is necessary to approximate the requisite condition by changing the solution at more or less frequent intervals. In order to determine exactly what has been the average condition of the solution between changes, analyses must be made as in the previously described experiments. Obviously the extent of change in the solution will depend upon the rate of absorption by the plant and also upon the concentration and total volume of solution per plant. Consequently, actual determinations of the quantity of each ion absorbed must be the basis for the selection of suitable culture vessels, number of plants, and times of changing solution. If too small a total supply per plant of any element is present, all or nearly all the ion in question may be removed from the solution in the interval between changes of solution. Since all of the ions are not absorbed in equal percentages, not only the total concentration of the solution but the ratio between ions will be changed. The average composition of the solution will depend then upon the particular set of empirical conditions chosen. How very important these considerations are is indicated by all the absorption studies of this investigation. It will be recalled, for example, that when two barley plants seven weeks old were placed in 1 liter of a solution of about 200 parts per million total concentration, in less than 72 hours every trace of NO_3 and over 90 per cent of the K and PO_4 were removed from the solution. It is quite clear from such an experiment that absolute quantities rather than concentration may have been the limiting factor. In fact a later experiment indicated that such was the case.

Brenchley (*5*) grew barley and wheat plants for seven weeks in solutions of 3,000, 600, 300, and 150 parts per million. The solutions were changed every four days. She concluded that the lower concentrations are sub-optimum and criticised Stiles' (*43*) results. The latter grew single plants in 1,200-cc. bottles for six weeks, changing the solution every three or five days and using concentrations of 1,750 parts per million and one-fifth, one-tenth, and one-twentieth of that concentration. He did not find a significant difference in yield, although there was some falling off in the lowest concentration.

Tottingham (*45*), as a result of various experiments by the water-culture method, using 250- or 400-cc. bottles with six plants to a bottle for a growth period of 23 days, decided on a concentration of 2.5 atmospheres as optimum, though he recognized that a less concentrated solution might give an equal yield.

Shive (*39*), with a technic similar to that employed by Tottingham except for the use of a 3-salt nutrient solution, came to the conclusion that 0.1 atmosphere was sub-optimum concentration and assumed the optimum concentration to be 1.75 atmospheres. This concentration has since been adopted by other investigators as optimum. In Shive's (*40, 41*) sand-culture experiments about 250 cc. of nutrient solution

remained in each jar after changing solutions. There were three to five plants in each jar.

Lyon and Bizzell (*25*) found that wheat seedlings gave increased growth with increasing concentrations from 83 to 4,525 parts per million total salts. They used 120-cc. bottles in the water-culture series.

Bouyoucos (*2*) also states that increased yields occur with increasing concentrations up to 4,500 parts per million. In his experiments 120-cc. bottles were used with four plants in each bottle. The period of growth was three or four weeks. Solutions were changed once each week.

Other experiments similar to these have been carried out, but these citations will suffice for the present purpose. The point which it is desired to emphasize now has been clearly stated previously by Stiles (*44*) in his criticisms of Brenchley's conclusions, but these criticisms have apparently been neglected in later work. In all of the above-mentioned experiments no sufficient distinction has been made between supply of nutrients and concentration of nutrients. If we compare the quantities of nutrients per plant available between changes of solutions with quantities of nutrients actually absorbed, as shown by data given in this article, we must conclude that in many cases the total supply may have fallen far short of the requirements, so that the solutions were constantly undergoing a great change, due to absorption. Moreover the relative changes may be very different in different solutions. For example, in those solutions in which only one-tenth of the total concentration was due to $Ca(NO_3)_2$ the NO_3 supply conceivably may have been entirely insufficient, whereas in solutions with a higher ratio of $Ca(NO_3)_2$ the supply of NO_3 may not have been exhausted. If all the ions were not absorbed in the same proportion, the result would be a continuously varying solution, with regard to both total concentration and ionic ratios. Without knowing precisely the nature of these changes it would seem difficult to interpret the results in terms of ionic ratios. Perhaps it is significant that in many cases the areas of low yields in the triangular diagrams have been found near the line of least $Ca(NO_3)_2$. NO_3 is the element of greatest importance quantitatively. In the following table some estimates are made of the total volume of solution per plant necessary to furnish total quantities of nutrients equal to those absorbed by the plant, under conditions permitting good yields of crop.

As another basis of calculation we may use the data for the sand cultures of series 1. It can hardly be denied in this case that a lack of total NO_3, K, PO_4 were limiting factors, and that the total yield per plant was greatly reduced by reason of these deficiencies. Yet even under these conditions the total quantities of nutrients found in each plant were 0.15 gm. K, 0.15 gm. PO_4, and 0.30 gm. N calculated to NO_3. To supply these quantities of NO_3 would require 1 liter per plant of a nutrient solution containing 300 parts per million of NO_3 or 20 changes

on basis of 50 cc. per plant. If in addition it were desired to maintain the solution at approximately the same concentration and composition at all times, many times this number of changes of solution would be necessary. In this general connection it may be noted that Trelease and Free (47) have given brief mention to an experiment in which it was found that higher yields were obtained in cultures with a continuous flow of solution.

TABLE XIV—*Approximate volumes of solution equivalent to total quantity of NO_3 absorbed per plant*

[Nutrient solution containing 300 parts per million NO_3]

Age of plant.	Solution required per plant in three days, based upon absorption by plant from soil.	Solution required per plant in three days, based upon absorption by plant in water cultures from nutrient solution of 2,200 parts per million concentration.
Weeks.	*Cc.*	*Cc.*
4 to 5	100	260
6 to 7	300	380
11 to 12	100	380

On basis of 50 cc. per plant, solutions would have to be changed from once daily to three or four times daily to provide the quantity of N calculated from above absorption studies. If K or PO_4 were present in low concentration, large volumes of solution would also be necessary to supply these elements in the quantities capable of absorption. To maintain approximate constancy in solutions, very much larger volumes than the foregoing might be required.

It is of course unjustifiable to apply at all rigidly absorption data obtained in one set of plant studies to another set, for the reason that temperature or light conditions may in some cases be so unfavorable that any large growth is impossible, and as a result absorption also will be greatly diminished because the plant is stunted. Moreover, in the first few weeks of growth absorption is comparatively slight; only when plants are grown six weeks or longer will the full extent of absorption become apparent. Some experiments dealing with concentrations and ionic ratios have not been carried on for a sufficiently long time to give an adequate idea of the effects of the various solutions tested.

The statement is often made in texts on plant physiology that entirely normal plants may be grown in solution cultures, but no data are given concerning the yield per plant of grain and total dry matter. In fact, only recently have detailed results been presented of systematic experiments in which plants have been grown to maturity. In most of the experiments the data and descriptions would indicate that the plants obtained were decidedly inhibited by some factor, the total dry weight per plant, height, number of tillers, etc. being usually less than for similar plants grown under favorable conditions in the field for an equal period. Various causes might be assigned to account for the diminished yields. Obviously light or temprature may be unfavorable, and enor-

mous fluctuations may be due to these factors. Possibly other conditions related to the physical nature of the medium may have an effect. There is also a strong presumption in certain experiments that the total supply of nutrients may limit the yield in the manner just outlined. In any case it would seem necessary to determine what are the limiting factors that prevent the production of an optimum plant. It is possible to obtain in sand and water cultures plants very similar in size to those given in productive fields under equal climatic conditions. The following data are evidence of this statement.

AIR-DRY YIELD PER PLANT.

Kind of culture.	Heads.	Stems and leaves.
	Grams.	*Grams.*
Water solution	8 to 12	10 to 19
Sand	10 to 15	12 to 20
Soil	5 to 14	11 to 26

The plants of the water- and sand-culture experiments referred to above were grown out of doors under light conditions similar but inferior to those obtaining in the soil experiments. In some instances the grain presented a more shrunken appearance in the sand and water cultures, though the total yield and proportion of heads to straw are not very different.

As a corollary to the foregoing discussion the conclusion is unavoidable that no sufficient evidence has yet been adduced to show that varying salt proportions within a wide range have any significant effect on yield. The validity of such deductions can not be established until the control of the nutrient solutions is more definite and until the interpretation of the data is made with due regard to the significance of variability studies, such as those proposed by Waynick (*53*).

In connection with any critical discussion of the interpretation of data from plant nutrition studies, one other factor must be considered—the relation of solution cultures to sand cultures. Upon this point the literature is in disagreement. Bouyoucos (*2*) found that solution cultures gave a higher yield than sand cultures with the same solution. Lyon and Bizzell (*25*) observed in certain experiments that sand cultures were superior to solution cultures and advanced the hypothesis that absorption took place around the solid particles, so that the plant really obtained its nutriment from a solution of higher concentration than that added to the sand. McCall (*27*) reached an opposite conclusion. He found that a smaller yield was obtained in sand cultures and that optimum ratio of ions was changed materially. This he attributed to absorption by the sand, changing the composition and concentration of the solution available to the plant. On the other hand, Shive (*40, 41*)

has not found that the sand had any marked influence when the same solutions are compared in sand and solution cultures. Wolkoff (*56*) confirms this point of view in general, although he finds that ammonium sulphate ($(NH_4)_2SO_4$) exhibits somewhat anomalous behavior.

During the present investigation a number of experiments were made relating to this question. Freezing-point determinations were made on nutrient solutions and on sand to which the solutions had been added to give the sand a moisture content of 15 per cent. Also solutions were allowed to stand in contact with the sand for long periods, conductivity determinations being made at intervals.

TABLE XV.—*Effect of sand on freezing-point depression and conductivity of nutrient solutions*

Freezing-point depression of solutions.	Freezing-point depression of sand immediately after adding solution.	Freezing-point depression of sand after 4 days.	Freezing-point depression of sand after 9 days.	Freezing-point depression of sand after 67 days.	Resistance of nutrient solution.	Resistance of nutrient solution with sand after 80 days.
°*C.*	°*C.*	°*C.*	°*C.*	°*C.*	*Ohms.*	*Ohms.*
0. 025	0. 032	0. 027	0. 028	....	198. 0	171. 0
. 145	. 145	. 149	. 149	0. 134	37. 5	37. 2

From the data given above there is no indication that the sand has appreciably altered the added solutions. To what, then, may discrepancies between sand and water cultures be ascribed? In the first place, a much more extensive root development takes place in the presence of the solid particles. This might in itself imply a different type of absorption, though plants in solution cultures are capable of sufficient absorption quantitatively under suitable conditions. Diffusion in water cultures is very rapid but must be somewhat retarded in sand culture. For this reason in the very early stages before an extensive root system has been formed solution cultures may be superior to sand cultures, while later the conditions may be reversed. Aeration is another factor which is different in the two cases. Hall and Underwood (*15*) claim that this is the chief difference between sand and water cultures. It is also conceivable that the larger root system of sand cultures might affect the growth of tops by the formation in the roots of a greater quantity of some substance accelerating growth. And finally, since even pure sand is not entirely insoluble, a greater supply of silica is available to the plant in sand culture. The exact effect of this is of course not known.

As a matter of fact, in our experiments no very striking differences are observed between sand and water cultures although it has generally been true that taller plants with a greater number of tillers are produced in sand cultures. Somewhat lower concentrations are inhibitive in solution cultures, though the magnitudes do not vary greatly, and the differences

found might reasonably be related to the extent of the root system and rapidity of diffusion. There is certainly no convincing evidence that selective adsorption by the sand plays any important rôle, although the exact relations still remain to be worked out. This can be accomplished only by comparing a sufficient number of plants under identical aerial conditions and with complete control of the solutions in all cases. Some preliminary indications suggest that the paraffin seal used in sand cultures may be slightly inhibitive to growth. This might be omitted in experiments planned to solve such questions as the above.

It will not be necessary to enlarge on the earlier discussion in this article with regard to the effect of hydrogen-ion concentration. The critical consideration of this phase of the work has already appeared elsewhere (*16–19*). It will suffice to emphasize the inapplicability of titration methods in determining the reactions of the nutrient solutions, and the fact that permeability or absorption are influenced by the hydrogen-ion concentration, although a P_H value of 5 has not been found to be inhibitive either in solution or sand culture nor in peat soils when other inhibitive factors are absent.

Finally, brief attention must be given to the methods of stating results, since these may in themselves modify the interpretation or planning of further experiments. The practice in these investigations has been to state the composition of the solutions in terms of parts per million of each ion. This seems to be the most logical scheme, since it is not possible to determine in such complex solutions the exact nature and concentration of the undissociated molecules and ions present. In most cases the dissociation values are high, and there is no satisfactory evidence to show that the ionic concentrations are not chiefly concerned in absorption by the plant. Certainly whatever the original salts used, the properties of the solution are those of the ions and molecules formed after solution has taken place. Thus we are of the opinion that it is desirable to compare solutions on the basis of parts per million of the various elements or radicles present rather than on that of molecular or osmotic fractions of the salts used in preparing the nutrient solutions. The latter method may lead to neglect of the factor of total supply of essential ions, as pointed out before.

In a recent article Tottingham (*46*) suggests as a result of some experiments performed in his laboratory that even with highly dissociated salts the particular salt used has an effect apart from the ions formed in the solution. It seems, however, that the evidence presented in support of this idea is insufficient. If a large number of plants had been used and the significance of the results evaluated, as in the previously mentioned work of Waynick (*53*), it is not apparent that the same conclusion would have been reached.

In the present investigation concentrations have been expressed for convenience in terms of atmospheres, derived from determinations of

freezing point depressions. It is realized, however, that such expressions are matters of convenience and not necessarily significant. The osmotic pressure of a solution is defined by Findlay (*10*) as the "equivalent of the hydrostatic pressure produced when the solution and solvent are separated by a perfectly semi-permeable membrane." The absorbing membranes of the roots are obviously not of this sort. They are permeable to all the ions present in varying degrees and, moreover, as shown by Osterhout (*1*, *p. 96–147*), the permeability is subject to change as a result of antagonistic relations among ions. It is also to be noted that the osmotic pressure and electrolyte concentration in the expressed plant sap are far greater than those of any noninjurious nutrient solution. The effects of solutions are not due to the theoretical osmotic pressures of which the solutions are capable, but rather to alterations in permeability due to specific ions or ionic relations, or to internal derangement of the metabolic processes as a result of a too great absorption of one or all ions.

SUMMARY

(1) Sand- and solution-culture experiments were carried out under conditions permitting definite control of the total concentration, composition, and reaction of the nutrient solutions. Numerous absorption studies were made throughout the growth cycle of the barley plant. Plants were obtained which were fairly comparable in size and development with those produced by a fertile soil.

(2) Marked absorption of all the nutrient elements took place at all periods up to the final stage of growth when suitable concentrations of the various ions were continuously maintained. This intense absorption during the later stages led to no important increase in yield of crop, which seemed to be conditioned in large measure on a favorable supply and concentration of nutrients during the first 8 or 10 weeks of the growth cycle.

(3) With increasing concentrations of the nutrient solution it was found in these experiments that the composition, expressed in percentages, and total quantity of N and K per plant were decidedly increased in the tops. This was also true for the roots, but in addition these showed a marked increase in the percentage and total quantity per plant of Ca and PO_4. In the tops most of the Ca, Mg, PO_4, and K was present in a water-soluble form. In the roots grown in the solutions of the higher concentrations large percentages of insoluble Ca and PO_4 were found.

(4) When plants of uniform development were transferred to nutrient solutions of different concentrations, a greater transpiration took place from solutions of low concentration. Absorption and transpiration took place independently, so that the solution under some circumstances might become either more or less concentrated, depending upon the original concentration of the solution.

(5) The optimum total concentration of the nutrient solution, if defined as the least concentration giving a yield equal to any higher concentration, was not found to be greater than that represented by 0.6 atmosphere osmotic pressure; and it may be less than 0.1 atmosphere. For the solutions used in these experiments, inhibitive concentrations were not higher than those represented by 2 to 2.5 atmospheres osmotic pressure.

(6) In the interpretation ofthe results of solution- and sand-culture experiments in terms of concentration and ionic ratios, emphasis is placed on the necessity of clearly distinguishing between the concentration and composition of the solution used and the total supply of the various elements provided for each plant. In the periods between changes of solution the concentration and composition may be markedly altered because of absorption by the plant. In many experiments the number of plants and size of culture vessels have been chosen arbitrarily without reference to these facts.

(7) From a consideration of previous experiments it is concluded that there is no sufficient evidence to prove that the plant requires for optimum yield any very specific ratio of ions or elements within wide limits, provided the total supply and concentration of essential elements are adequate.

(8) In solutions with an acid reaction (P_H 5 to 5.5) the absorption of several ions was greater than from a neutral solution (P_H 6.8) of similar composition and the same total concentration.

(9) One experiment suggested the possibility that at certain periods of growth excretion of electrolytes may take place, and that this phenomenon is dependent on the reaction and concentration of the nutrient solution.

(10) An acid reaction represented by P_H 5 was not found to be injurious to the barley plant at any period. There was a tendency toward the production of a neutral reaction in the solution as a result of changes in the equilibria due to absorption.

(11) When the plant was placed in a very dilute nutrient solution, excretion of electrolytes, especially Ca, Mg, PO_4, took place at first. This was followed by absorption which continued until the solution had a resistance comparable to that of the distilled water used in making the solutions.

(12) There was no evidence that the sand used significantly altered the concentration or composition of the nutrient solution. Other reasons are suggested for differences between sand and solution cultures.

(13) The mode of expressing the composition and concentration of the nutrient solution is discussed, and it is suggested that the theoretical total osmotic pressure of the nutrient solution is not necessarily significant in its relation to the plant. It is also concluded that the interpretation of results should be based on the composition of the solution in terms of ions or radicles rather than of the salts used in preparing the solution.

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